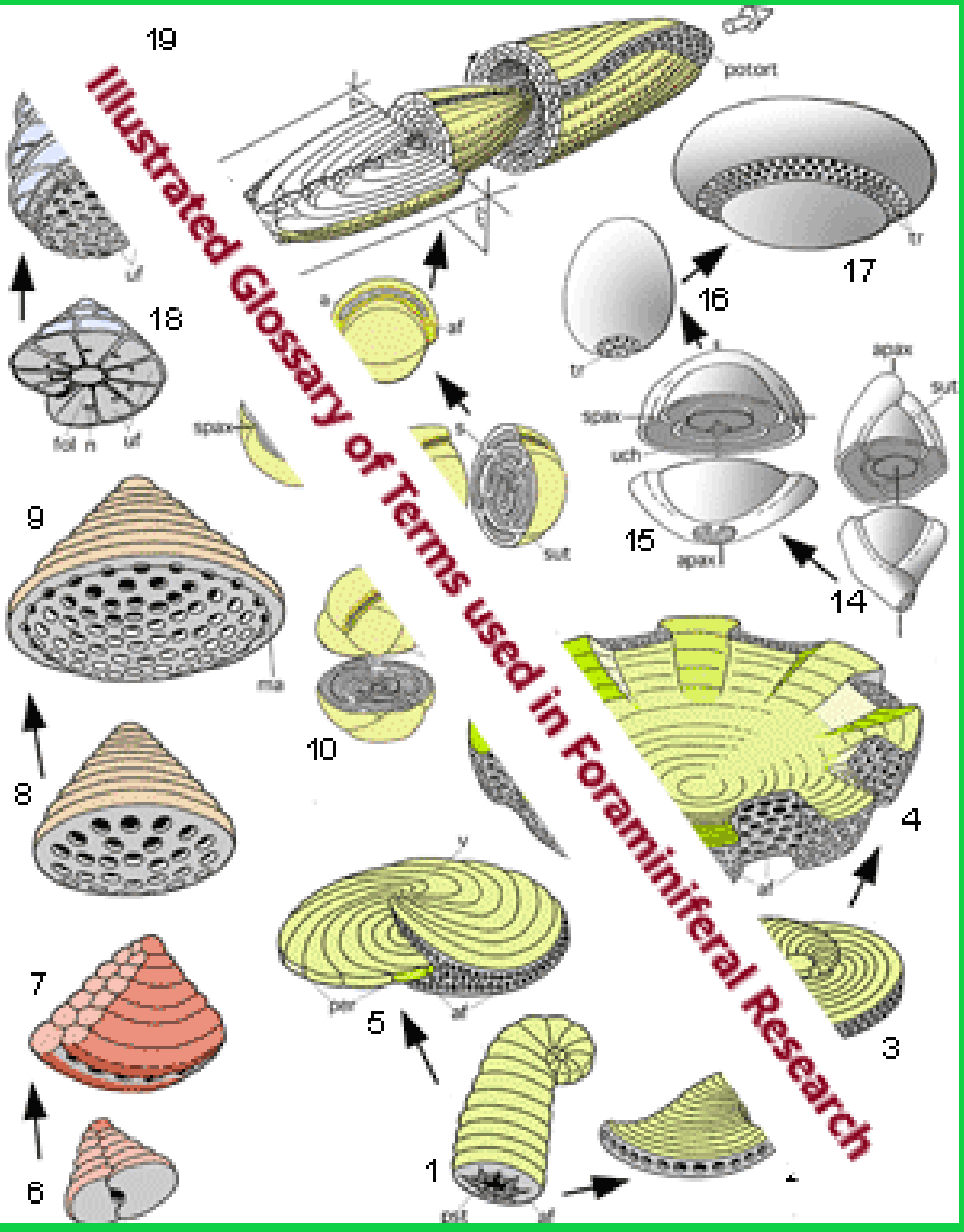
Illustrated Glossary of Terms used in Foraminiferal Research



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Introduction
Nature and significance of specialized terms

Diagnoses and descriptive texts of taxa demand the use of a specialized terminology to embrace in a reasonably short and manageable text the complex morphology of any taxon. Pictures of the object described are necessary to supplement its description in words. In many cases however the "description" is restricted to the specification of diagnostic features, often without an indication of their location in the illustration or photograph. An ideal description requires that a reasonable number of specimens per taxon be illustrated at the same scale and with the same orientation. This procedure helps the eye to distinguish, because of the repetition of diagnostic characters, those features that define the taxon from intraspecific variations. Desirable descriptive texts support this process by pointing out what to look for. But no matter how well illustrated such a "description" may be, the use of an explicit terminology cannot be avoided.

Most distinctive morphological characters have been named through the coinage of specialized terms. They may be based only on geometrical features in the second or third dimension, or may include in their concept biological processes such as growth or reproduction. For example: what is a "chamber"? and what is a "chamberlet"? in radial foraminifera (**DROOGER**, 1993). According to a concept based on the geometry of the cavities in the shell, neighboring lumina in an annular cycle that are not in direct communication are called "chambers". A concept including growth would consider that all cavities in the annulus have been formed at the same instant and would call them "chamberlets". All cavities of the annulus would form a chamberlet cycle and correspond to an undivided annular chamber. Thus, terms based on common concepts help to avoid comparing "apples and pears". They are the basis for the comparative anatomy of foraminiferal shell structures introduced by **DOUVILLÉ** (1906).

Accurate description of foraminiferal architecture began in the second half of the 19th century (**CARPENTER**, **PARKER** & **JONES**, 1862) but the biological meaning of many morphological features of the foraminiferal shell was discovered only in the second half of the 20th century. Thereafter a considerable evolution in terminology has taken place. To day, the electronic treatment of data plays an ever-increasing role in science. As yet, the machine is not able to recognize the context in which these terms are used.

In contrast to Linnean taxonomy, where the principle of priority contributes enormously to the stability of the taxonomic system, an introduction of priority to morphological terms would block all progress in understanding the complex morphology of the shells, their morphogenesis and their biological, functional and evolutionary meaning. However, wherever it is possible and meaningful the use of the most widely recognized term is recommended in order to stabilize, as far as possible, and to standardize diagnoses and descriptions.

There is a major parallelism in the terms used to describe fusulinids of the Late Paleozoic on one hand and of larger nonlamellar-imperforate benthics from the Mesozoic and Cenozoic on the other. This parallelism was generated by the traditional specialization of the respective researchers; so far, very few have been active in both fields. Although the concept of a suborder Fusulinina separating most of the Late Paleozoic benthic foraminifera from the later clades is supported by the largest biological turnover in Earth History at the end of Permian times, there is no reason to use discrete morphological terms with regard to major divisions of geological time, for throughout the Phanerozoic many characteristics of th shell are common to all foraminifera. The present glossary may help to unify some of the parallel terms to a common usage.

Current terminology used by various authors in describing the morphological features of the foraminiferal test is far from being uniform and varies greatly from case to case (compare *e.g.* **REISS**, 1963; **HOTTINGER**, 1967, 1978; **HOTTINGER** *et alii*, 1993; **LOEBLICH** & **TAPPAN**, 1964, 1987). The reasons

for the coinage of several terms for the same feature are in most cases not at all formal, but due to one or more of several factors: differences of opinion with regard to the significance of a named element as it relates to homologies and analogies; differences in the degree of observational accuracy; differences in the methods used to prepare samples for examination (**HOTTINGER**, 1978). In some cases, the terms are based on the geometry of shapes as they appear in a particular orientation of a section rather than on their three-dimensional geometry. The employment of such terms may be misleading and is not recommended.

The terms listed in the following Glossary are accompanied [in square brackets] by alternative terms and (in parentheses) by terms considered to be synonymous, partially synonymous, unclear or to be avoided for other reasons. Where in my own experience the translation of a term into French or German is difficult, the translation is indicated in (parentheses). The plural of terms coined in Latin, such as foramen, are indicated by: , pl. foramina. Biological terms are selectively included in the number considered essential to an understanding of the foraminifers and the biological significance of their shell structure. Some specific ecological terms are defined and discussed to facilitate understanding of the increasingly abundant literature concerning the ecology and biogeography of foraminifera. Current discussions on the "**Paleonet**" list [**http://jerwood.nhm.ac.uk/archives/paleonet/**] show that the presentation of some basic terms used in taxonomy, biostratigraphy and evolutionary theory may be helpful.

The taxa of a generic or higher level used to portray the meaning of a term or to illustrate the range of its application are from **LOEBLICH** and **TAPPAN** (1987). For taxa that are not a generotype, additional specific references are given in the text. Clicking in the alphabetic index brings up illustrations of the taxon in question that may help to verify an identification.

The hierarchy of basic architectural elements in benthic foraminifera

Using basic concepts of biomineralisation and wall construction (**HOTTINGER**, 1986; **BENDER**, 1989) that include the lamellar theory of **SMOUT** (1954) and **HANSEN** (1999), chamberwise growth, reproduction, comparative anatomy (**DOUVILLÉ**, 1906; **REICHEL**, 1936-1937; **HOTTINGER**, 1978), and functional morphology including the demands of symbiosis with unicellular algae (**HOTTINGER**, 1997), a hierarchy of the most important morphological terms can be formulated. On each hierarchical level, the terms for wall elements, cavities and connections between them are specific. They should not be used out of their hierarchical context.

1. Elements not modifying the shape of the living protoplast:
1.1. wall **textures** indicative of one of the several processes of biomineralization
1.1.1. agglutinated walls with noncalcareous cements binding the grains
1.1.2. intracellular biomineralization
1.1.2.1. calcareous cements binding agglutinated grains
1.1.2.2. porcelaneous walls
1.1.3. extracellular biomineralization: lamellar wall
1.2. wall **textures** produced by discrete arrangement and/or composition of constituents of the wall
1.2.1. wall polarity outside-inside
1.2.1.1. transition gradual, no layers: tectum, epiderm, pavement, endoskeletal textures (in basal layers for example).
1.2.1.2. transition abrupt, wall layered, produced by a single or double-sided organic template: inner and/or outer lamellae (lining)
1.2.2. differentiation of repetitive elements perpendicular to wall surface: parapores, pits, keriotheca, pseudokeriothecal textures, pores, pore chimneys. Opening of pores at wall surface: pore mouth; internal polygonal modification housing symbionts: eggholders.
1.3. **ornaments** produced by repetitive differentiation of external wall parts or layers: ribs, spines, pseudospines, spikes, pustules, beads, papillae, piles.
2. Elements modifying the shape of the living cell by chamber-wise growth:
2.1. incorporation of frontal shell walls including aperture(s) into the shell by adding a new compartment to the previous shell, a new **chamber** (with its **aperture**). First chamber: proloculus; second chamber (if not differentiated from later ones): deuteroloculus. Added

cavity: chamber lumen; separating wall: septum; connection between successive chamber lumina: intercameral foramen, if tubular and multiple: stolon, if generated by resorption and wide open: tunnel.

2.2. subdivision of chamber lumen by deformation of chamber walls: fluting (including cuniculi) if frontal; retral lobes or processes if affecting the posterior chamber wall.

2.3. subdivision by circular invaginations of lateral parts of the chamber wall by calyces or similar structures in expanse chambers.

2.4. generation of multiple chamber lumina within a single growth step, enclosed by the same primary wall: chamberlet cycle.

3. Generation of shell shape (cylindrical, conical, globular, fusiform, lenticular) by **chamber shape** and **arrangement**:

3.1. serial disposition of chambers: uniserial, biserial, triserial.

3.2. spiral disposition of chambers: streptospiral, planispiral, trochospiral, multiple spirals.

3.3. milioline chamber arrangement.

3.4. by modification of chamber shape: chevron-shaped, involute, evolute, concentric (in two dimensions): annular, concentric (in three dimensions): spherical-concentric.

4. Elements modifying the shape of the protoplast in the chamber lumen:

4.1. elements independent of protoplasmic flux as revealed by patterns in subsequent foramenal disposition (arrangement of foraminal axes): **exoskeleton**. Cavities: compartments such as alveoles, subepidermal networks, alcoves; separating walls: beams (perpendicular to septum), rafters (parallel to septum); connecting open chamber lumen between exoskeletal cavities: passages.

4.2. elements reflecting protoplasmic flux by conforming to foramenal features and patterns: **endoskeleton**. Cavities: compartments, if more or less closed: chamberlets; separating shell elements: if free standing and circular in section: pillar, if forming a wall perpendicular to primary chamber wall: septulum, if a free standing wall: hemiseptulum; if covering the previous septal face only: septal flap; if covering at the chamber bottom previous septal faces and/or surfaces of previous shell whorls: basal layer; connecting open chamber lumen between compartments: passages.

5. Shell cavitites produced by (lamellar) growth covering interlocular space: **supplemental skeleton**. Cavities: if tubular: canals, if more or less isometric: supplemental chamberlets

5.1 cavities produced by separation of the frontal wall of the previous and the proximal wall of the subsequent chamber: intraseptal interlocular space, may be subdivided into intraseptal canals

5.2 cavities produced by a space between subsequent whorls of a spiral array of chambers: spiral interlocular space, often restricted to a more or less tubular spiral canal. Opening of canals at shell surface: orifice.

5.3. cavities produced between subsequent whorls of spiral chambers and structures filling partially the umbilical space: umbilical interlocular spaces or canals.

5.4 cavities produced by infolds of outer lamellae over peripheral parts of spiral chambers or chamberlet cycles: marginal interlocular spaces (marginal cord, marginal crest, canalicular spines).

6. Branching canalicular cavities running obliquely through subsequent, regularly perforate outer lamellae: trabeculae.

7. **Embryonic apparatus** different in architecture and/or structure as compared to adult parts of the shell:

7.1. first or first two or three septa straight, uncurved, different from the adult: bi-, tri- or quadriconchs.

7.2. tubular extension of protoconch foramen (flexostyle) eventually feeding a particular deuteroconch with multiple apertures (vestibule).

7.3. concentric deuteroconch enclosing an often poorly calcified protoconch with an exoskeleton: sphaeroconch.

7.4. hemispheric deuteroconch with exoskeleton (supraembryonic chamber) feeding a cycle of nepionic chamberlets with exoskeleton only (subembryonic chamber).

7.5. multilamellar envelope of embryo enclosing several chambers and feeding a particular cycle of first (nepionic) chamberlets (corona, with auxiliary and adauxiliary chamberlets).

Glossary

A

A - form – see gamont, schizont.

abaxial - directed away from or far from the shell axis.

aboral – directed away from or in a position opposite to the apertural [oral] end of shell.

accessory aperture (infralaminal aperture, auct.) - aperture that does not lead directly into the main chamber lumen, but extends beneath accessory structures (*e.g.* in bullae). Fig. 1.

acervuline - chambers in irregular, clustered arrangement, as in *Acervulina*.

acicular - needle-shaped.

acicular spine - see spine.

actin – cytoplasmic protein producing in its polymerized form short, contractile fibers. If positioned below the cell wall, they may form stellar arrays.

acuminate - tapering, *i.e.* getting thinner or pointed; conical.

acute - shape with acute or sharp angles.

adapertural depression (periapertural depression; cavity; apertural fissure, sulcus, auct.) - space formed by a toothplate that separates it partly or completely from the main chamber lumen. Interconnected adapertural depressions produce a canal. Fig. 2.

adauxiliary chamberlet - chamberlet arising from a single radial stolon (additional with respect to the apertures between proto- and deuteroconch) in the embryonic wall of orbitoidiform shells. Fig. 4.

adaxial - directed towards or positioned near the shell axis.

adventitious - produced by or with the help of foreign particles such as those forming an agglutinated test.

advolute chamber arrangement - in those spirally coiled forms where the chamber lumina of a whorl cover laterally those of the preceding whorl to a considerable extent, but not entirely, on one or both sides. Fig. 3. Compare: evolute,

agamogony - asexual reproduction within the reproductive cycle, from the first mitotic division of the zygote to meiosis. Fig. 5.

agamont - specimen grown from the zygote, producing either gamonts or schizonts in an asexual process involving apogamous nuclear divisions and/or meiosis. Foraminiferal agamonts, produced by a sexual reproduction, are called microspheric (B - form). Fig. 5. See also: brood chambers, Fig. 24.

agglutinated - shell texture characterized by components gathered in the ambient environment and bound by organic or biomineralized cements produced by the cell. Particles may be selected according to size and shape to form a closefitting mosaic. Often, the agglutination in the external and internal parts of the wall is differentiated but there are no sharp boundaries (see also wall polarity). Fig. 6.

alar prolongation - winglike extension of umbilico-lateral portions of involute chambers on lateral surfaces of previous whorls in lenticular tests. May be meandering. Fig. 7.

alcove - a blind compartment of a chamber lumen delimited by beams and the lateral chamber wall, as in *Orbitopsella*. Fig. 72.

allopatric speciation - emergence of species by geographic isolation of populations for a time sufficient to alter the genome of the populations involved to a mutual reproductive incompatibility.

alternating arrangement of shell compartments – Shell compartments (chambers or chamberlets) of successive growth stages arranged on alternating radii of the shell. Fig. 8.
Remarks:. The alternating arrangement of the shell cavities is a very fundamental and widespread pattern of the foraminiferal architecture. It occurs in all three dimensions: the first, linear dimension (= biserial), the second, planar dimension, in annular-concentric shells, in particular in the main layers of orbitoidiform groups, and in the third, spatial dimension, in shells with spherical concentric growth, where it forms chessboard patterns at the surface of the globular shells.

alternation of generations - see life cycle. Fig. 5.

alveolar layer - layer of alveoles in lateral chamber walls forming diagnostic exoskeletal structures lacking a differentiation into beams and rafters as well as polygonal subepidermal patterns; distinct from subepidermal, polygonal networks or keriothecal textures. See exoskeleton (Fig. 45) and keriotheca (Fig. 62).

alveole (alveolus, pl. alveoli) - a recess of varying depth in lateral walls, coated by the organic lining, blindly ending with a rounded contour below an epiderm or some equivalent outer layer of the wall and opening into the chamber lumen. May branch towards the outer part of the wall, each generation of branches forming layers within the wall. Fig. 9.
Remarks: The term alveole is used here exclusively for exoskeletal structures, *i.e.* for subepidermal, tiny compartments of the chamber cavity coated by an organic lining. Alveoles are supposedly filled with chamber plasm. Alveoles must be distinguished from paraporous or parakeriothecal cavities that are an adjunct of wall texture. Like true pores, these cavities are (by definititon) neither filled with living chamber plasm nor coated by the organic lining. The simultaneous presence of both alveolar structures and keriothecal wall texture in the fusulinid *Verbeekina* and its relatives, the combination of an alveolar exoskeleton with a paraporous external wall in *Dicyclina* or with a bilamellar perforate wall in *Fabiania* supports a consequent restriction of the term's use to exoskeletal structures, never to textures.
Layers of alveoles coating the lateral chamber wall are present in various agglutinated groups of which *Cyclammina* is the most prominent while *Everticyclammina* is an early extinct representative of an exoskeletal layer of exclusively undivided, shallow alveoles. The Neogene group of *Textulariella* **CUSHMAN** (**GRÖNHAGEN** & **LUTERBACHER**, 1966) has branching alveoles. Among the porcelaneous foraminifera with alveoles, *Austrotrillina* is a prominent group. In this genus, species with deep and branching alveoles - *A. howchini* (**SCHLUMBERGER**) - are said to evolve from earlier forms with layers of shallow, undivided alveoles (**ADAMS**, 1968). The term alveole is also used for rows of blind recesses in postseptal position over supplementary apertures in the previous septal face as in *Subalveolina* or *Bullalveolina*. We do not yet know, how to interpret (in terms of exo- or endoskeletal elements) these alveoles nor what might be their biological meaning.

analogous – similarity in function and, where shape is functional, also in shape, of independent ontogenetic origin and hence of different evolutionary origin. See also homologous, homomorphous.

annular arrangement - arrangement of concentric annular chambers.

annular canal - free space in preseptal position between endo- and exoskeletal structures in spirocyclinids.
Remarks: Unrelated to canal systems in lamellar perforate foraminifera. The term should not be used but replaced by annular passage.

annular chamber - ring-shaped chamber. May be subdivided as in *Cycloclypeus*.

annular passage [annular stolon] - annular, open space in preseptal position, may be single, in the equatorial plane, as in *Sorites*, or double, in lateral position, as in the archaiasines. In orbitoidiform foraminifera the adjacent lumina of a chamberlet cycle may be connected by a pair of tubiform lateral passages in postseptal position (lateral annular stolons, as in *Discocyclina*, Fig. 41 A) or by several layers of annular stolons ("six-stolon system" as in advanced *Eulepidina*). See also: preseptal passage.

annulus - ring-shaped chamber, which may be subdivided, or ring-shaped cycle of chamberlets. See chamber arrangement, Fig. 37.

anterior - directed to or positioned near or on frontal part of chamber, usually including the main aperture, distal in respect to direction of growth.

antetheca - apertural face in fusulinids.

apertural axis – the shell axis defined by a placement of foramina in a single line. See milioline coiling, Fig. 68.

apertural chamberlet – the cavity in preseptal position below the radiate aperture in *Lenticulina* and related forms. The lamellar nature of the wall between the main chamber and the apertural chamberlet remains unclear at present.

apertural face – that surface of the chamber-wall that contains the main cameral aperture. See also face, septal face, umbilical face, Fig. 48.

apertural flange - see lip.

apertural lip - see lip.

apertural plate [basal plate] - a plate-like structure that restricts the base of an interiomarginal aperture and restricting the latter. Fig. 10.

apertural tooth - see milioline tooth and valvular tooth.

aperture – the primary opening of the foraminiferal shell cavity towards the ambient environment. May be covered by subsequent chambers and thus transformed into a foramen. May be masked (see mask). May be single or multiple. Fig. 48 (See also cameral aperture; foliar aperture; supplementary aperture; labial aperture).
Remarks: We insist here on restricting the use of the term "aperture" in chambered shells to the ultimate opening of the last chamber cavity into the ambient environment. When a new chamber is added to the previous one as a main process of growth, the aperture is transformed into a means of communication between successive chamber lumina and thus its function changes. The transformed aperture is called a (intercameral) foramen. Its morphology may change through selective resorption of its margins. Often, the last chamber of the shell is not preserved because of its thin walls (see lamellation) and the aperture is lost.

apex - initial portion of trochospiral or conical test.

apical - referring to the initial part of a trochospiral or conical test.

apogamous – reproducing according to the mode of apogamy.

apogamy – the process of reproduction where the offspring has the same number of chromosomes as the parent cell.

arborescent – in permanently attached shells, a tree-like, branching growth pattern. Fig. 11.

areal - positioned within the apertural face, neither at its base nor at the shell margin.

areal aperture - cameral aperture in a distal wall, not at a suture. May be single or multiple. Fig. 12.

arenaceous - see agglutinated.

areolate – the chamber wall is subdivided into more or less equal surfaces (areoli) as in *Homotrema*. Fig. 11.

asexual reproduction - a mode of reproduction where the genome of a single individual is duplicated.

astral fissure - see folium, foliar aperture, foliar suture.

astral furrow - see foliar suture.

astral lobe - see folium.
Remarks: **CARPENTER** *et alii* (1862), **BRADY** (1884) and in particular **DAVIES** (1932) in his basic monograph on *Rotalia trochidiformis* used the term astral lobe (Fig. 13) to designate what is currently called a folium. In spite of their similar ventral-adumbilical position astral lobes must be distinguished from stellar chamberlets (as in Amphisteginidae) that are separated from their corresponding main chamber by a complete wall. However, functional similarities may not be excluded.

attachment – the permanent fixation of a shell onto its substrate. See also surface of attachment, arborescent growth, encrusting growth, Fig. 60.

attics (French: mansardes) – in porcelaneous shells the outermost lateral or abaxial layer of chamberlets in a multi-layered endoskeleton, distinguished from less lateral or adaxial ones by the comparatively small caliber of the tubiform chamberlets, as in *Alveolinella*. Fig. 14.

autogamy – a process of sexual reproduction where amoeboid gametes from the same gamont mate (in foraminifera within the mother shell) to form a zygote. May be combined with ogamy.

auxiliary chamber [or **auxiliary chamberlet**] – a chamber or a chamberlet fed by a stolon positioned in the suture between protoconch and deuteroconch in orbitoidiform foraminifers. May be double in embryos with a bilateral symmetry or multiple, when the protoconch and the deuteroconch have additional equatorial stolons. Together with the adauxiliary chamberlets, they form a corona. Fig. 4; Fig. 36.

auxiliary tunnel – the coalescence of several subsequent cuniculi as in *Polydiexodina*.

axial filling - secondary deposits in narrow spaces around the axial columella in fusulinids and pfenderinids.

axial plate – see umbilical plate, cover plate.
Remarks: This term, introduced for *Ammonia* by **CIFELLI** (1962), was substituted erroneously by **PARVATI** (1971) by "umbilical plate" but in fact is a cover plate. Continued use of the term "axial plate" would add to the considerable confusion in the current concepts of rotaliid umbilical architecture (see also **LÉVY** *et alii*, 1986).

axial section – a slice bisecting the test in a plane coinciding with the axis of coiling and intersecting the proloculus. Compare equatorial section. Fig. 15.

axial septulum - an exoskeletal structural element parallel to the septum in verbeekinid fusulinids and consequently corresponding to the rafter in the exoskeletons of other agglutinated and porcelaneous foraminifera.

axis of coiling – an imaginary line around which a spiral test is coiled. Fig. 7 & Fig. 68. See also chamber arrangement.

B

B - form – see agamont.

balloon chamber – a hemi- to sub-spherical chamber surrounding a float-chamber in the pseudoplanktic stage of some benthic foraminifera; provided with multiple openings for extrusion of gametes. Fig. 16.

basal - at the base or parallel and proximate to the base of a structural element or of a complete architecture.
Remarks:. The term is occasionally used for interiomarginal apertures or foramina at the base of the apertural face adjacent to the previous whorl (in contrast to areal) or for the base of a cone in conical shells including sections in or parallel to the base of the cone. Fig. 80 B. See also basal layer.

basal disc - the thickened but porous extension of the median layer in the proximal pore cavity that is part of the pore plug. Fig. 75 A-B.

basal flap – in milioline forms an interiomarginal, spathulate, more or less excavated infold of the distal wall projecting into the aperture and restricting it. Fig. 17.
Remarks: The basal flap in miliolids seems to be an extension of the basal layer detached from the previous whorl and extending into the large aperture. It may be a homologue of the milioline tooth.

basal layer - in imperforate foraminifera: the parts of a chamber wall coating the previous coil and/or the septal face of the previous chamber. As they are not in contact with the ambient environment, these portions of the wall lack the differentiations in the texture of the outer wall. Basal layers represent or are part of the endoskeleton, and may be sculptured by ribs in the chamber lumen or form endoskeletal elements reaching the ceiling of the chamber, *i.e.* pillars or septula. Fig. 18.
Remarks: The basal layer is a very important element of the architecture of imperforate foraminifera. In spiral-involute and miliolid shells it may become much thicker than the external chamber wall (flosculinisation); in fusiform shells it may form a double columella reaching both poles of coiling. Thickened basal layers often have numerous tubular passages of irregular shape connecting successive chamber lumina, with (edomiids) or without (elongate alveolinids) intermediate preseptal spaces. In our view the basal layer is homologous with the "basal skeleton" of fusulinids (chomata and derived structural elements). Where tubular chamberlets are vertically superposed, the basal layer may form regular floors parallel to the chamber roof, as in elongate *Praealveolina*.

basal lobe - a finger-like extension of a chamber wall at the spiral or septal suture (in the absence of an interlocular space). (See retral lobe and compare ponticulus).

basal skeleton - see chomata.

basement – cavities below a main chamberlet layer, developing polewards in elongate alveolinids, delimited by floors and septula, opening into a preseptal space and connected vertically by shafts, as in *Praealveolina*. Fig. 70.

bead – a small, rounded to hemispherical protuberance on the surface of lamellar shells, forming strings along septal, septular or hemiseptular sutures. Usually imperforate or poorly perforate. To be distinguished from papilla. Fig. 73.

beading – strings of beads along linear shell elements such as sutures. To be distinguished from costellae.

beam – an exoskeletal main partition of the chamber lumen, perpendicular to the chamber septum and to the lateral chamber wall. In discoidal shells often separated from an endoskeleton by an empty space in the chamber (annular passage). May fuse with endoskeletal elements such as septula,

particularly in verbeekinids, orbitolinids and cuneolinids. May occur as unique exoskeletal element (*Orbitopsella*, Fig. 72) or in combination with minor, shorter exoskeletal elements producing a subepidermal polygonal network (Spirocyclinidae, Fig. 45).
Remarks: **DAVIES** (1930) distinguished "primary" or "major" (1939) partitions in the description of orbitolinids in opposition to "secondary" or "minor" elements. **HENSON** (1948) separated "subepidermal plates" from main partitions (the latter being of endoskeletal nature and therefore to be called septula nowadays; compare **HENSON**'s fig. 7, reproduced here as Fig. 19). **HENSON**'s (1948) subepidermal plates, synonymous with **SILVESTRI**'s "trabecole perpendicolari" (1932), were subdivided again into "transverse" and "parallel" partitions corresponding to **DAVIES**' major and minor elements. **HENSON**'s general term "subepidermal partition" may include main partitions (= septula), transverse partitions (= beams) and parallel partitions (= rafters), where septula and beams fuse to produce (mostly radial) chamber compartments. In order to distinguish partitions according to their origin, **HOTTINGER** (1967) introduced particular terms for partitions exclusively of exoskeletal origin, *i.e.* "poutre" for major and "poutrelle" for minor partitions, translated into English in 1978 as "beam" and "rafter" (Balken and Bälkchen in German). For illustration see exoskeleton.

biconcave - test having both sides concave (in coiled forms).

biconch - protoconch and deuteroconch together, if separated by a straight septum, thus differing in shape from later, curved ones. The straight septal wall suggests that hydrostatic pressure in protoconch and deuteroconch was equal as a morphogenetic control before the wall was calcified. Thus, the two first chambers were formed together and represent a single growth stage similar to an embryonic apparatus.
Remarks: The status of a biconch as a particular growth stage is supported by **RÖTTGER**'s (1974) observation that biconchs in nummulitids are formed after hatching, *i.e.* after the naked embryo is squeezed out of the narrow canal orifices. In such biconchs, the second chamber is used to keep the few symbionts transmitted from the mother shell in their first stage of procreation within the new generation of their hosts. Other embryos calcify their shell with straight septa beween the first two, three or even four chambers within the mother shell and will leave it during the hatching process by dissolving chamber walls of their mother.

biconvex - test having both sides convex (in coiled forms).

bifid - divided into two branches. See also milioline teeth.

biformed - change in chamber arrangement during ontogeny, for example from coiled to uncoiled or triserial to bi- or uniserial.

bilamellar wall - in perforate foraminifera a chamber wall formed primarily by two mineralized layers (outer and inner lamellae) on either side of a primary organic sheet, the median layer. See also lamellar wall, outer lamella, inner lamella.

bilateral - having two equal sides by mirror symmetry.

bilocular - said of an embryonic apparatus having two chambers differing in size and shape from the following ones.

biloculine - see milioline coiling. Fig. 68.

bipartitor – a bridge-like structure, extending posteriorly from an umbilical plate, crossing the preceding aperture and attached to the adjacent coil, thus cutting off the intercameral foramen from the opening into a primary umbilical canal. Fig. 21.

biserial - trochospiral chamber arrangement with about 180° between consecutive chambers, thus producing two rows of chambers. See serial disposition of chambers. Fig. 37.6-7.

biumbilicate - spiral test having umbilici on both sides. Fig. 22.

biumbonate - having an umbo on both sides of the test.

blades - plate-like, strongly protruding, short or long costae. Fig. 23 A.

blueprinting – a morphogenetic process: repetitive induction of shape by preexisting shapes, such as linear angularities or shoulders on a previous chamber that induce the position of the suture of the following chamber, or of areal reliefs by protrudent pile heads on which subsequent lamellae are thickened.

boss – see umbo. Compare: plug; pile.

brood chamber - chamber(s) or chamberlet cycle(s) with enlarged cavities that house the offspring before hatching. The enlarged chamber cavities may be produced by partial resorption of shell material, in particular of the endoskeleton and the septa. To date, brood chambers have been observed exclusively in agamonts (microspheric specimens). Fig. 24.

buccal aperture - see funnel.

buccal ring - see chomata.

bulla – a blister-like test element extending over the umbilicus of the ultimate whorl and covering primary, main or supplementary apertures. May have marginal accessory apertures. Present in planktic foraminifers only. Fig. 1.

buttress - see pillar.

C

calyx, pl. calyces (pillar-pore) – a funnel-shaped, perforate invagination of lateral wall supporting expanse chambers over a wide area as in *Miniacina*. Fig. 25.

cameral [chamber] **aperture** - single or multiple opening in a chamber-wall that allow the communication of a main chamber lumen with the ambient environment. It may later be converted partially or entirely into an intercameral foramen, unless that foramen has been formed secondarily by resorption. The position of apertures on the apertural face (interiomarginal, marginal, areal, umbilical, extraumbilical, terminal) and persistent patterns in multiple apertures (see endoskeleton) are of fundamental taxonomic value. See also supplementary aperture; foliar aperture, tunnel, mask. Fig. 48.

canal systems - a term collectively and broadly applied to those interconnected spaces of the foraminiferal test, that are primarily or secondarily separated from the main chamber lumina, but with which they may communicate in one or in successive whorls by openings other than intercameral foramina, the so-called loop-holes. Canal-systems contain functional microtubular ectoplasm and represent bypasses of spiral main chamber lumina so that ectoplasm deep inside the early parts of the test connects directly with extrathalamous rhizopodial ectoplasm. The spaces forming canal-systems are delimited by a number of discrete elements of the test: umbilical plate, cover plate joined to a foramenal plate, sealing plate, toothplate, septal flap, folia, previous coil, as well as by consecutive outer lamellae. See also: primary and secondary umbilical spiral canals; intraseptal interlocular spaces; grooves; enveloping canals; funnels; cord, crest. Fig. 26.

canalicular structure – a structural pattern produced by repeated modes of canal disposition in the foraminiferal shell. See also: canal system.

canaliculate crest - see crest.

canaliculate [canaliferous] **spine** – a spine- or club-shaped to arborescent radial structure composed of consecutive outer lamellae enclosing canals (supplemental skeleton). May contain spikes. Compare pseudospine; spine. Fig. 27.

cancellate - having honeycomb-like surface ridges as ornament. Fig. 28.

carina [keel] – a peripheral thickening of the shell. May be doubled in Cretaceous planktic foraminifera. In bilamellar foraminifera formed exclusively by the outer lamella and therefore imperforate. Fig. 29.

cell envelope in foraminifera - all elements covering the living cell body of a foraminifer delimited by its plasmalemma.

cell wall – biomineralized cover of living cell.

central complex – see reticular zone. Adaxial cone in conical agglutinated forms where radial septula are fused to an irregular pattern of meshes. In contrast to radial zone and marginal zone. Fig. 20 & Fig. 71.

chamber [loculus] – the space and its enclosing biomineralized walls formed at one instar, *i.e.* during a single step of nepionic and ephebic growth. See also: chamber lumen, chamberlet.

chamber arrangement – the pattern of disposition of chambers in a shell. Fig. 37.

chamber lobe - see folium.

chamber (or chamberlet) **lumen** – a shell cavity filled with protoplasm (usually of an endoplasmic nature except in newly formed chambers), coated by an organic lining, the primary cell envelope. By definition, chamber lumina communicate exclusively through intercameral foramina and/or multiple stolon systems. The term "chamber lumen" is used in particular to distinguish between the "inside" and "outside" of a shell, *i.e.* between intra- and interlocular spaces. The latter are never papered with an organic lining. Within the boundaries of intraspecific variability the volume of chamber lumina may depend on the seasonal availability of food and be independent of wall thickness which in lamellar foraminifera is dependent on water turbulence.

chamber passage - see passage.

chamber wall(s) - skeletal elements formed at one and the same instar, enclosing the corresponding chamber and coated by an inner organic lining.

chamberlets - segments or subdivisions of a chamber, produced during the same instar. See also: subsidiary chamberlets; cycle of chamberlets; foliar chamberlet; lateral chamberlets; stellar chamberlet.

chamberlet cycles – the chamberlets forming an annulus within one instar. The annuli may produce a single layer thus forming a disc, as in *Planorbulinella*, or in a lenticular shell be comprised of a main chamberlet layer with lateral layers of chamberlets or lateral expanse chambers, as in orbitoidiform architecture. The chamberlets of an orbitoidiform that cycle in alternating radial positions may or may not be connected by annular passages. However, they are always connected indirectly by the retrovert stolons feeding the lateral chamberlets. Fig. 36.

chessboard pattern – a chamberlet arrangement in superposed chamberlet layers in alternating positions resembling those of a chessboard: in one layer, the position of the chamberlets corresponds to the black fields, in the following layer to the white fields, as in *Sphaerogypsina*. The outline of the chamberlets may be quadratic, polygonal or somewhat irregular. This three-dimensional array corresponds to the annular chamberlet arrangement, that is alternating radial positions in the second dimension. Fig. 8 F-H.

chevron shape – the inverse of V- shaped. See also: equitant.

chirality – the proportion of right-hand to left-hand coiling in a population of trochospiral organisms, as seen from the spiral (dorsal) side. See dextral and sinistral coilings.

chloroplast (plastid) – the organelle of a plant cell (in foraminifera endosymbiontic algae) that are responsible for photosynthesis, with ultrastructures (thylacoids, pyrenoid) of different pigmentation diagnostic for several algal groups. Fig. 30.

chloroplast husbandry – a particular symbiotic relationship in which chloroplasts of ingested algal food cells are kept in the host protoplasm in a state of partial functionality. Fig. 30.

choma (pl. chomata; German: Basalreifen) – a dense deposit on previous whorl constituting the chamber floor, and in fusulinids forming a pair of parallel ridges, each extending from a tunnel margin to the previous one. May extend progressively polewards over the entire chamber floor in staffellids, much like a basal layer in fusiform porcelaneous shells. Fig. 31.

chomatal pores – porelike texture of chomata in higher fusulinids as continuation of pore-like textural elements in the keriotheca or parakeriotheca below the tectum of the previous whorl. Fig. 66.

circumproloculus – a deuteroconch that in some advanced fusulinids envelops the megalosphere to a large extent.

clavate - club-shaped.

climax – end of an ecological succession, when an equilibrium with the long term ecological conditions is reached.

closing chamber – a symmetric interauxiliary chamber. See chamber arrangement in orbitoidiform foraminifera. Fig. 36.

coalescence – the fusion of separate, elongated parts.

coenocline (community gradient) – the distribution of populations of species in ecological gradients.

cohort – a demoecological term for a group of individuals conditioned in their temporal development by a common event in the ambient environment. In foraminifera: the individuals produced by a more or less synchronous hatching triggered by seasonal change, and without reference to their mode of origin, *i.e.* agamonts or schizonts which differ greatly in length of life.

coil - see whorl.

coiling axis - see axis of coiling.

columella – the solid, trochospiral structure formed by the basal walls of spiral chambers coalescing around the coiling axis, as in many gastropod shells, or symmetrically poleward in planispiral - fusiform shells. May be thickened by secondary deposits or by an extensive thickening of a basal layer in the polar realm of the shell (alveolinids). Fig. 32.

compartment – the lumen of the shell housing chamber protoplasm, communicating with other lumina in the shell by constricted passage-ways. Supposedly functions as a reactor receptacle for cell metabolism. A chamber may constitute a compartment or be subdivided into chamberlets that are units of a compartment. Compartments may have specific shapes. Tubular and isometric shapes do not occur together in the same taxon and may reflect different types of bioreactions. The volume of the compartment remains comparatively stable throughout growth but may be modified by the availability of food during the seasonal cycle. On the other hand, the number of compartments produced during one growth step may increase during ontogeny. Narrow passage-ways between compartments, stolons or foramina, may be temporarily closed by organic plugs, thus isolating the compartment's protoplasm from other compartments and in particular from the one containing the nucleus.

congeneric - belonging to the same genus.

conspecific - belonging to the same species.

contrefort – a lateral thickening of the inner wall layer against the base of the chamber lumen that thins or vanishes in the equatorial plane, as in some archaediscids. May be homologous with basal layer.

convolute - see evolute.

corona - first cycle of chamberlets enveloping an embryonal apparatus completely, at least in one plane of sectionning, as in *Discocyclina*. Fig. 41 A.
Remarks: The term may be useful in biometry when describing the relation between the diameter of the embryonic apparatus and the number of chamberlets in the immediately succeeding growth stage. See also: periembryonic chamberlets.

cosmopolitan - Occurring all over the world where ever there is a suitable habitat, the contrary of endemic.

costae - raised ribs or ridges on test surface. See also: striae, blades. Fig. 23 B.

costate - having costae.

costellae – a particular ornament on the chamber wall produced by more or less elongate ridges formed by an aligned fusion of pustules produced by secondary lamellation.
Remarks: The term was introduced to describe the particular ornament of *Costellagerina*, a rugoglobigerinid from the late Cretaceous. It might be useful to extend the term as a description of the radial ornamentation of the ventral chamber walls in smaller benthics indicating **ogamy** (pairing of two gamonts venter against venter), as in *Glabratellina*. Fig. 23 C-D.

cotype – see type.

counterseptum – a kind of lower lip of an interiomarginal - basal aperture appearing in appropriate sections as a forward directed hook below the foramen and glued to the previous shell whorl, as in *Eulinderina guayabalensis* (**NUTTALL**) or *Amphistegina lopeztrigoi* **PALMER** (**BUTTERLIN**, 1987). The hook is said to develop into "complete septal walls" in *Helicostegina*. Fig. 33.
Remarks: The term was introduced by **BARKER** and **GRIMSDALE** (1936) for proximal portions of the main chamber septum below the main foramen in *A. lopeztrigoi*. The hook may be identical with the gutter in Old World amphisteginids. The nature of the "complete", helicosteginid countersepta remains to be analysed the more so as the relation between "countersepta" and stellar septula in the New World amphisteginids is not clear.

cover plate [umbilical cover plate] (retroparies, pars auct.) - a more or less folded, imperforate extension of the septal flap into the preceding chamber through the intercameral foramen, separating - in the preceding chamber - the main chamber lumen from a foliar chamberlet. Usually attached to a preceding foramenal plate. It is a secondary feature, never present in the ultimate chamber and thus not homologous with a primary foramenal plate or umbilical plate. Compare also: sealing plate. Fig. 34.

cribrate - perforated by multiple holes. Should be used exclusively for numerous and small multiple apertures. See also trematophore.

cruciform - cross-shaped (aperture).

crystalline cone – see pile of lamellae; compare papilla.

cubiculum (pl. cubicula) – a lateral shell cavitiy in spiral and annular-concentric shells with a main chamber- or chamberlet- layer.
Remarks: This term, introduced by **BANNER** and **HODGKINSON** (1991) and exemplified by *Spiroclypeus*, "orbitoid, miogypsine and other, three-layered rotalines" is a substitute for what is traditionally called lateral chamberlets in larger foraminifera (compare **FERRANDEZ**, 1999). Apparently, **BANNER** and **HODGKINSON** mean by "true" lateral chamberlets in heterosteginids their alar prolongations subdivided into chamberlets. They

show them only in axial or transverse sections where the distinction between septal and secondary subdivision of shell cavitiesis is difficult to carry out. I suspect these "lateral chamberlet" to be undivided alar prolongations cut at an oblique angle in respect to the median line of the alae. See also: lateral chamberlet, supplemental chamberlet.

cuneate, **cuneiform** - wedge-shaped, as in *Cuneolina*.

cuniculus (pl. cuniculi; cunicular passage) - in fusulinids a transverse passage at the chamber base, parallel to the tunnel, connecting the lumina of alternating chambers. It is produced by the fusion of opposed folds in adjacent septa that lose contact with the previous whorl at their point of fusion. The geometry of the apertural face in cunicular fusulinid shells remains unclear. Fig. 35.

cupule – radial, rounded ridges on the shell face of conical shells resulting from an arrangement of slightly inflated radial chamberlets alternating in radial position in subsequent cycles.
Remarks: the term "cupule" means "cup" in French and English and refers to the cup-shaped sections perpendicular to an elongate barrel vault forming the radial chamberlets as in *Orbitolinopsis*, *Orbitolinella* or *Halkyardia*.

cycle of chamberlets - multiple segments of a main chamber lumen, produced at one and the same instar. Fig. 36.

cyclical arrangement - arrangement of cyclical chamberlets in one plane or in concentric layers. Fig. 8 C-H & Fig. 37.

cyclical chamberlet - one of the cyclical segments of the main chamber-lumen produced at one and the same instar. Fig. 36.

cyclopsinellid structure - arrangement of endoskeletal elements as in *Cyclopsinella*: the arrangement of endoskeletal pillars following the pattern of the radial stolon axes superposed in a radial position in neighbouring stolon planes. This particular pattern has a tendency to produce a more or less complete fusion of the pillars into a median shell wall. Fig. 47 F.

cyst – a temporary cover enveloping part of the shell, the whole shell or several individuals, consisting of adventitious material bound together by organic material or slime, as a protection of chamber building or of reproduction processes. Accumulations of refused food particles in front of the face at the margin of discoidal shells are called feeding cysts.

cytoplasm - protoplasm, excluding the nucleus.

D

dendritic - see arborescent.

deuteroconch – the second chamber in an embryonic apparatus. See also: sphaeroconch. Fig. 38.

deuteroloculus – the second chamber in a shell without embryonic differentiation, *i.e.* lacking an embryonic apparatus.

dextral coiling – a clockwise direction of coiling, as seen from the spiral side.

diaphanotheca – a light-colored or translucent wall layer immediately below the tectum in fusulinids. Fig. 39.

dimorphism - coexistence of two discrete morphotypes representing different generations in the life cycle of a single species. They are expressed in the adult growth stages and/or in the protoconch and in the following nepionic chambers. The protoconch diameter is large (megalospheric = A - form) when the agamont's protoplasm is distributed (including eventual symbionts) among the cloned offspring. The protoconch diameter is small (microspheric = B - form) when the gamont's gametes fuse pairwise to form a zygote whith no protoplasm or symbionts from the mother. If there is

dimorphism in the adult shell, the B - form becomes larger than the A - form. The compartments of the microspheric initial phases are small. It takes many growth steps to reach the initial shell size of the megalospheric generation. Reaching the adult oversize of the microspheric generation demands numerous additional instars. Consequently, the dimorphism of foraminiferal generations reflects different life times and thus different strategies of life within the same species: the microspheric generation is adapted to the permanent basic low-level carrying capacity of an oligotrophic and warm environment, while the megalospheric generation with its short life time adapts to both spring and eventual autumn seasonal peaks of carrying capacity. See also: odd pairs. Nepionts with large megalospheres may have a particular architecture different from that of the adult (see megalospheric apparatus). In complex life cycles, a third (schizontic) generation may produce megalospheric shells with a morphology slightly different from that of the gamonts. See also: trimorphism. Fig. 5 & Fig. 70.

diploid – a genome with paired chromosomes, one coming from the father, one from the mother. See also: haploid.

disclimax – an ecological succession truncated by periodical ecological events, as for instance the destructive turnover of hard substrates by winter storms.

distal - farthest from the proloculus in direction of growth.

distal chamber wall - farthest, in direction of growth, chamber wall.

distal face - outer surface of distal chamber-wall. See also: face.

distinctly radial texture – the appearance under crossed nicols of test wall fragment producing a dark cross of interference and concentric colour rings. Corresponds to fibrous ultrastructure.

dorsal - the side of a free, flattened organism turned away from its substrate, as opposed to ventral. See also: spiral side; umbilical side.
Remarks: **REVETS** (1994) rightly points out that the terms dorsal and ventral, beyond their specific meaning in the architecture of vertebrates, refer to the orientation of a flattened organism in respect to its substrate. In foraminifera, benthic, free shells live with their apertural face on their substrate in order to gather food. Permanently attached shells, usually filter feeders, are living with their apertures turned away from the substrate. They must have free apertures in order to add new chambers during growth. In most free, trochospiral forms, the spiral side is in a dorsal, the umbilical side in a ventral position. Nepionic, spiral stages in permanently attached forms (*Planogypsina* (Cibicididae) for instance) show by the position of their foramina in the early spiral whorl that their surface of attachment is on their spiral (dorsal) side. However, in current uage the terms dorsal-ventral and spiral-umbilical respectively may not always be synonymous.

E

ectoplasm – the microtubular outer zone of cytoplasm, that also forms the pseudopodia. They have many functions for movement, catching and transport of food, removal of excretory products and of gametes from the mother shell, in sensory tasks, in gas exchange, as well as in the processes of test formation. See also: canal systems.

egg-holder - internal pore mouth, enlarged to a cup with polygonal rims, with or without spinose projections at the junction with adjacent pores. Harbours symbionts in order to enhance the gas exchange of the symbiont with the ambient environment of the host. Fig. 30 and Fig. 40.

elongation index - in alveolinids and other fusiform or otherwise elongate shells, the ratio of the length of the axis of coiling to the diameter at the equator. Fig. 78.

embryo(n) [embryonic apparatus] – the group of chambers including protoconch and deuteroconch (nucleoconch), and in some genera a flexostyle, that differs in size, shape and arrangement from subsequent chambers. Fig. 41 A.

embryonic – the earliest growth stage in foraminiferal ontogeny, usually distinguished from later stages by an abrupt change in shell architecture, commonly with thickened walls indicating a longer period of cessation in growth as frequent in the megalospheric generation of larger K-strategists (bi- and triconchs; embryonic apparatus).

embryonic apparatus - see embryo(n).

embryonic pseudochamber ("Zwischenkammer" in **GRELL**, 1954) – a hemispherical cavity between the deuteroconch and a third chamber seen on the dorsal side of the shell as hemicircular protrusion.
Remarks: The "true", *i.e.* lamellar nature of this cavity and its connection with the regular spiral chambers seen in Rotaliellidae (see also **PAVLOWSKI** *et alii*, 1992) is not yet known.

encrusting growth – the mode of growth of permanently attached shells covering large surfaces by keeping low and close to it, accelerating the occupation of a surface by forming annular expanse chambers (as in certain species of *Gypsina*), in competition with rhodophyceans for instance. See also arborescent growth, surface of attachment.

endemic - occurring in restricted geographic areas; the contrary of cosmopolitan. Compare: vicarious species.

endoplasm – the central part of protoplasm containing the nucleus or nuclei and in which the major metabolic processes take place.

endoskeleton - localized thickenings on the inner surface of the chamber wall that partly or totally subdivide the main chamber lumen in the lee of protoplasmic streams according to a pattern produced by the arrangement of intercameral foramina in successive septa. Plate-like elements (septula), usually perpendicular to the septum, may form more or less complete partitions touching the lateral walls or fusing with elements of the exoskeleton. Discontinuous, columnar partitions are called pillars (or interseptal pillars). A third type of endoskeleton is produced by layers of shell deposited on the chamber floor and coating the previously exposed outer shell surface completely (basal layer) or partially (chomata and parachomata of fusulinids). In different taxa, the three endoskeletal types may occur alone or in varying combinations. Fig. 47 & Fig. 63. Often, endoskeletal elements appear only in the course of ontogeny, usually later than exoskeletal elements. In agglutinated shells endoskeletal elements include the septum and may be recognized by remarkably coarse and irregularly shaped particles that obscure the genetically fixed pattern in contrast to the more ordered exoskeletal elements of the same specimen. Whether the toothplates and their equivalents in lamellar perforate foraminifera and the secondary septa produced by folds of the inner lamella in orthophragminid lamellar architecture are homologous equivalents of the endoskeletal structures of non-lamellar-imperforate foraminifera remains an open question.
Remarks: The term endoskeleton was introduced by **H. DOUVILLÉ** (1906, p. 593 and 602) in a key paper comparing the anatomy of imperforate fusiform shells, *i.e.* fusulinids, loftusiids and alveolinids. **DOUVILLÉ** had already recognized the close morphological relationship between apertural and endoskeletal patterns. In his monograph on alveolinids, **M. REICHEL** (1936-1937) adopted the term endoskeleton to designate the structural elements subdividing the chamber in contrast to a so-called exoskeleton comprising the lateral and frontal chamber walls including the apertural face. The strict correspondence between the pattern of distribution of the foramina on the septal face and the patterns produced by the endoskeletal elements (in the alveolinids by the septula) were clearly demonstrated by models of the shell cavities and their connections through the septum as if they were a cast of the shell cavities (**REICHEL**, 1936-1937, fig. 27). These patterns are still used today as diagnostic features for the definition of alveolinid genera.
HOTTINGER (1967) modified and extended (1978) **DOUVILLÉ**'s term to include all structures subdividing the chamber lumen and linked to the patterns of intralocular protoplasmic streaming in contrast to exoskeletal partitions that are not affected by such patterns. Thus, the originally descriptive term is expanded to include a functional meaning and extended to all corresponding features in imperforate shells. In some lamellar-perforate foraminifera, comparatively rare structures (such as the hollow pillars in *Chapmanina*) correspond in shape and position to the definition of endoskeletal features. There is no reason to interpret their function otherwise. So such features may be called endoskeletal without hesitation. They may lead the way to clarify, by comparisons, the significance of true toothplate structures.

entosolenian tube [endosolen] – a tube-like internal skeletal structure extending from the aperture in a proximal direction. Fig. 43.

enveloping canals (intramural cavities, auct.) - more or less tubular spaces parallel with the test surface formed within lateral chamber walls and communicating with intraseptal interlocular spaces. The enveloping canals are produced by (non-adhering) imperforate portions of outer lamellae, that also cover partly the intraseptal spaces and are fold into these spaces, leaving on both sides of this "flying cover" alternating rows of openings for ectoplasmic flow over grooves in the perforate wall, situated between imperforate inflational ridges (feathering). Fig. 44 & Fig. 65.

ephebic - "adult", *i.e.* a post-nepionic growth stage during which the features characterizing the shell architecture remain constant. The ephebic stage may grade into a later gerontic stage where the architectural features risk becoming irregular, or are altered to form brood chambers, as is often observed in the microspheric generation of larger, complex foraminifera. See also: gerontic stage.

epiderm – the thin, outermost coat of a foraminiferal non-lamellar, imperforate chamber wall if it differs in texture from that of the inner layers. Present in all exoskeletons consisting of a polygonal network as in orbitolinids (s.str.) and spirocyclinids. May be homologous with the tectum of fusulinids. Fig. 45.

epiembryonic - see subembryonic.

epiphyte – Organism living on vegetal substrates. Larger porcelaneous foraminifera prefer seagrass leaves to algal thalli because the leaf-hairs (trichomes) give them hold on their surface. Fig. 42.

epitheca - biomineralized deposits on inner chamber surface in fusulinids, comprising tectorium and chomata.

equator(ial) – the peripheral line in the median plane, perpendicular to the axis of planispiral coiling or to radial symmetry in chamber arrangement.

equatorial aperture – an interiomarginal primary chamber aperture in spiral tests, straddling the equatorial periphery.

equatorial chambers or chamberlets - see main equatorial chamberlets.

equatorial crest – in discocyclinids the equatorial thickening of the inner lamella of the equatorial main chamberlets. Fig. 41.

equatorial section – a slice of the test in the equatorial plane. Fig. 37.13.

equitant (in German "reitende" Kammer) - uniserial arrangement of chevron-shaped chambers, more or less embracing the flanks of the preceeding ones, as in *Flabellina*. Foraminiferal chambers of this type, usually with a single, terminal aperture, are commonly two-dimensional, as in *Flabellinella*, rarely three-dimentional, as in the Permian *Colaniella*. Biological significane unclear. Fig. 49.

eucaryote – a cell with a complete, membrane-coated nucleus housing a set of single (haploid) or double (diploid) chromosomes.

euphotic zone - the water layers in which light penetration permits the photosynthesis of eucaryotic cells, to about 140 m depth in pristine water bodies (blue deserts).

evolute chamber arrangement - in spirally coiled foraminifera where - due to chamber shape - the chamber lumina of a coil do not cover laterally those of the preceding coil. Fig. 7. Compare involute.

exocytosis – expulsion of fluids and solids from the cytoplasm into the ambient environment through the cell membrane.

exoskeleton - localized thickenings on the inner surface of the chamber's outer walls that subdivide the chamber lumen into blindly ending compartments. They form geometric patterns which are independent in number and direction from those determined by protoplasmic circulation through foraminal systems, *i.e.* endoskeletal patterns. Exoskeletal elements may consist simply of partitions (beams) perpendicular to the septum and to the

lateral chamber wall, that produce simple alcoves, or of a tapestry of alveoles of various kinds coating the internal surface of the outer chamber walls. Two main alveolar types may be distinguished: 1) branched or unbranched alveoles with a blind ending of rounded outline below the external wall surface: the partitions lack a differentiation into beams and rafters and 2) pigeon-holes with a blind ending polygonal in outline below an abaxial, that is produced by partitions differentiated into beams and rafters. Fig. 45. Exoskeletal elements may be very deep, subdividing the chamber almost completely as in *Dictyopsella*.
Remarks: **M. REICHEL** (1936-1937) introduced the term "expressis verbis" as a contrary of **DOUVILLÉ**'s "endoskeleton" for alveolinids. He thus designated the free, outer chamber walls including the frontal wall with its apertures as exoskeletal, all internal partitions (septula, basal layer and chamber floors) as endoskeletal. This concept was supported by an obvious differentiation of the wall texture in the external cover of the chamber walls considered at that time to be mainly the expression of a particular "behaviour" in the diagenetic process. Nowadays, we know that this particular kind of differentiation in the porcelaneous wall is textural and corresponds to the general differentiation of all lamellar-perforate and non-lamellar walls into inner and outer layers.
In agglutinated foraminifera, there are often true structural elements to be classified in separate categories in much the same geometric way as **REICHEL** conceived it, for they carpet the internal surfaces of the free lateral chamber walls (exoskeleton) or follow the foraminal pattern in the septa (endoskeleton). In discoidal agglutinated shells, exoskeleton and endoskeleton are separated by open spaces running parallel to the septum, the annular passages. In uniserial-conical constructions, the main radial partitions of a chamber may be continuous, extending from the shell center to the periphery of the chamber and comprise an inner, endoskeletal and an outer, exoskeletal part (as in *Orbitolina*). Thus, **REICHEL**'s (1936-1937) term exoskeleton was conserved but its definition restricted to true structures as opposed to the also exclusively structural elements of the endoskeleton (**HOTTINGER**, 1967, 1978). Therefore, the endoskeleton as conceived here comprises septal structures only when such elements consist of blind-ending recesses carpeting also the lateral chamber walls (*Hottingerita*) or when more complex structures derive from such a feature (*Alveosepta*). **BANNER**'s "hypodermis" (1966, according to the English manuscript) is not synonymous with "exoskeleton" but a general term for all kinds of alveolar layers, including the pigeon-holes of the polygonal subepidermal network, but excluding simpler "pseudalveolar" structures as in *Orbignya* or *Voloskinovella*. As the distinction of polygonal networks and various alveolar structures is of great taxonomic and stratigraphic importance, we do not recommend the use of the term hypodermis.

expanse chamber (dome-shaped chamber, auct.) – a chamber extending over a wide area above a previous chamber and adhering to it in a vermiculate or reticulate pattern. Fig. 46.

extrathalamous - situated outside the test.

extraumbilical aperture - an aperture in the primary chamber of coiled shells situated at the interior margin but not connected with the umbilicus.

extraumbilical-umbilical aperture – an aperture located on the interior margin of the primary chamber of a coiled shell that extends from the umbilicus to the periphery.

F

feathered – ornamented by numerous parallel grooves extending in more or less perpendicular direction from sutural furrow or fissure onto shoulders of ventral chamber walls, as in many rotaliids. Fig. 50.

face – a differentiated part of the shell surface delimited by modification of shell shape, of wall texture or of ornamentation, where single or multiple primary apertures and/or orifices of interlocular spaces are grouped to form a functional unit. Fig. 48.
Remarks: Sofar, the term "face" has been used in combination with a modifyer like apertural face or septal face, that concern only a single chamber. In addition, we introduce here the generalized term "face" to designate that portion of the shell surface which by its morphological differentiation indicates a particular function. This surface may be delimited by breaks in the topography of the shell surface, such as an angular periphery in trochospiral shells that delimit a more or less flattened base to the conical shape of the shell, or by a particular wall texture, the lack of perforation for instance, and/or by

a discrete ornamentation such as radial (*Discorbinoides*) or parallel-linear (*Scarificatina*) ornaments over spiral-umbilical surfaces. Faces are directed towards the substrate in motile benthics, away from the substrate in permanently sessile, arborescent forms or are opposite each other in paired shells ready for plastogamy. The grouping of apertures and/or orifices on the face may indicate its autecological functions.

feeding cyst – pads or rolls of the remains of digested food that accumulate temporarily in front of apertural faces of benthic foraminifera. May contain identifyable particles such as coccoliths or diatom frustules indicating elements of the diet of the foraminifer.

fistulose chamberlet (marginal chamberlet; peripheral chamberlet auct.) - in agglutinated foraminifera the space produced through separation either peripherally or laterally of part of the chamber from the main chamber-lumen by a paraporous partition. May occur in species with either solid or paraporous walls. In the latter case, the partition is a continuation of the paraporous inner wall-layer beneath the outward turning outer, solid layer, the pavement. Fig. 51.

flabelliform - fan-shaped.

flagellum – a tubular extension of the cell, reinforced with microtubuli and anchored by centrioles deep inside the protoplast of dinophycean symbionts. The short flagellae are used for locomotion in the lacunar system of the host as a device for regulating irradiation intensity in order to avoid photoinhibition. Fig. 30 B.

flange (French: collerette) – a thin, fragile marginal portion of an orbitoidiform shell where the main chamberlet layer is exposed for lack of lateral chamberlets. Fig. 52.

flexostyle (French: goulot) - in porcelaneous foraminifera an eaves-like extension of the proloculus wall that forms a space, u-shaped in section, over part of the proloculus. Fig. 41.

float-chamber – a large hemi- to subspherical chamber that facilitates floatation, found in the pseudoplanktic stage of some benthic smaller foraminifera. Occurs inside a so-called balloon chamber. Fig. 16.

floor (French: plancher; German: Boden) - Part of endoskeleton: wall parallel to basal layer separating superposed, regular chamberlet layers in alveolinids. Fig. 14 & Fig. 70 G-H.
Remarks: Advances in the comparative anatomy of alveolinids and miliolids requires that superposed regular layers of chamberlets separated by floors (= planchers, **REICHEL**, 1936-1937) as in *Praealveolina* or *Alveolinella* be distinguished from irregular, tubular, supplementary chamberlets present in a thickened basal layer as in *Alveolina* or *Subalveolina*. Both regular supplementary chamberlets and irregular, tubular chamberlets appear as soon as the fusiform shell reaches a specific minimum elongation (**HOTTINGER**, 1962). In particular the irregular chamberlets of *Alveolina* appear during ontogeny, at first in very low numbers, in shells where the polar thickening of the basal layer has produced an elongation of 1.4 : 1 in axial length versus equatorial diameter. A relationship between elongation index and polar structure is observed also in the parallel phyletic lineages. However, the difference between regular supplementary chamberlets and irregular-tubular passages in the polar columella is as diagnostic as all other structural features.
When **HAMAOUI** and **FOURCADE** (1973) were revising the axially compressed relatives of the classical alveolinids, they described the basal layer pierced by tubular supplementary passages as "central thickening". **REICHEL** (1984, fig. 3, p. 530) established the homology of the thickened basal layer in the polar area of *Subalveolina* with the "central thickening" of *Rhapydionia*. *Chubbina* was described by **ROBINSON** (1968) as having tubular passages in a basal layer, while **DE CASTRO** established (1990) *Pseudochubbina* as the taxon for a compressed alveolinid "with floors". In published illustrations, the *Chubbina* endoskeleton rather resembles that of an advanced *Praealveolina* with floors while *Pseudochubbina* has, particularly in adult growth stages, very irregular tubular passages in a massive basal layer. Thus, the unfortunate current use of the term floor is synonymous with basal layer. A detailed structural analysis of laterally compressed alveolinids (**FLEURY** & **FOURCADE**, 1990) will be necessary to distinguish precisely the two kinds of endoskeleton.

flosculinisation – a conspicuous thickening of the basal layer in the equatorial zone of miliolid and alveolinid shells. Fig. 18.
Remarks: The term was derived from the ancient generic name *Flosculina* **STACHE** by **SCHWAGER** in 1883. Flosculinisation occurs not only in alveolinids but in other, unrelated porcelaneous genera as well. It may be restricted to a particular period of ontogenesis, or sometimes to two successive stages, and be combined with a polar thickening of the basal layer.

fluting (septal fluting) - folding of the septa at their base in fusiform shells, as in fusulinids. The folds in consecutive septa oppose each other and may fuse at their bases, thus loosing contact with the surface of the previous whorl that is the chamber floor and consequently producing passageways parallel to the tunnel, the so-called cuniculi. Fig. 35.

foliar aperture (labial aperture, pars auct.) – the primary opening of a folium to the exterior in an interiomarginal anterior, posterior or umbilical (axial) position at the folium borders; it lies between the main chamber wall and the folium (foliar slit; astral fissure); or in the folium itself. A foliar aperture may be a continuation of the primary cameral aperture or separate from it, but it is never converted into an intercameral foramen. It may lead to funnels when covered by secondary lamellae. Fig. 53.

foliar chamberlet – the part of a chamber delimited by a folium. A foliar chamberlet may be continuous with the main chamber, and is separated primarily (and partly or more completely) from the main chamber by a foramenal plate, by an umbilical plate, or - secondarily - by a cover plate or a sealing plate. A foliar chamberlet communicates with the exterior through foliar apertures and with the lumen of its own main chamber through openings in the umbilical plate or cover plate (when present) or at its margin. Depending upon the geometry of the test, a foliar chamberlet may be converted into part of a secondary spiral umbilical canal as part of the umbilical cavity and communicates with intraseptal interlocular spaces. Fig. 53.

folium (lip; tenon; umbilical flap; astral lobe, pars auct.) - in spiral lamellar foraminifera an axial-umbilical portion of the lateral chamber wall, generally triangular in outline and often texturally differentiated (porosity). The limit between the main lateral chamber wall and the folium may be marked by a short, posterior indentation or "notch" and/or by an umbilical plate-suture. An opening (foliar aperture) is always present between the anterior margin of a folium and the adjacent previous coil. In addition, umbilical and/or posterior openings may be present, depending upon whether the folia are free or attached by their tips or along their posterior margin. In some genera such as *Asterorotalia*, the folia may extend onto the preceding chamber and be attached to it, partially covering intraseptal interlocular spaces wherever present. A folium is composed of the same layers as those forming the wall of the main chamber. See also: foliar chamberlet; foliar aperture. Fig. 53.

foramen [intercameral foramen] (plural: foramina) – the opening or openings that allow communication between the lumina of consecutive chambers and provide passage for functional endoplasm. May be primary, hence formed by an initial cameral aperture, or secondary, *i.e.* formed by resorption of masks or other parts of the septum (tunnel). Cameral apertures converted into intercameral foramina may be modified in shape by resorption or through restriction by attachment of a toothplate, foramenal plate or umbilical plate. See also: stolon.

foramenal axis - an axis common to two or more intercameral foramina or stolons in subsequent septa; may form regular patterns. Fig. 47 & Fig. 80.

foramenal disposition – the pattern generated by a regular spacial disposition of foramina on septal faces. Fig. 47 & Fig. 80.

foramenal plate (toothplate; paries proximus, pars auct.) - basically a primary infold or "inpush" in the direction of growth of the posterio-lateral chamber wall at a sutural notch, and attached to a single intercameral foramen. A foramenal plate is a detached continuation of a septal flap that may or may not be connected with a cover plate in the previous chamber. A foramenal plate separates to some degree the main chamber lumen from the lumen of the foliar chamberlet and the chamber plasm from the ectoplasm in the interlocular spaces. Compare: umbilical plate; bipartitor. Fig. 34.

fore-court – a deuteroconch with multiple apertures covering the outer flexostyle opening and parts or all of the wall of the megalosphere in complex soritid embryos. Introduced by **LEHMANN** (1961) under the German term "Vorhof". Fig. 41.

fossette – the opening to the exterior of an intraseptal interlocular space which is subdivided by ponticuli with retral processes. Fig. 54.

four-stolon system (or pattern) – a pattern of the stolon arrangement of arcuate chamberlet cycles that alternate in radial position from one cycle to the next and are connected by 2 oblique stolons to both the preceding and following cycles.

foveolate - see pits, pitted.

funnel (vertical canal) – a tubular (interlocular) space more or less normal to the test surface produced by secondary lamination over several whorls. Funnels originate from the margins of sutural canals or fossettes, or of foliar apertures communicating with a spiral-umbilical canal. Vertical canals persist in secondarily laminated parts of the test as long as they are not covered by later chambers. Fig. 55.

fusiform – the outer shape of a shell similar to a spindle, with its polar ends more or less tapered (see shell shape, Fig. 37.13). In fusulinids, loftusias, alveolinids, *Fusarchaias* and *Boreloides*, it is produced by planispiral-involute growth when the length of successive chambers in axial direction increases more rapidly than the half circumference of the corresponding equator of the shell. Note the shortening of the pathways through a fusiform shell in polar direction for up to one order of magnitude as compared to the equatorial path and see also polar torsion.

G

gametogamy – a process of sexual reproduction in which gamonts release their flagellate gametes into the free water column, where they mate.

gamogony - sexual reproduction within the reproductive cycle, from meiosis to fecundation, generating the zygote.

gamont – a specimen producing gametes in the process of reproduction irrespective of its involvment in meiosis (diploid gamonts) or not (haploid gamonts). Foraminiferal gamonts, produced by asexual reproduction are megalospheric (A - form).

gamontogamy – process of sexual reproduction where two gamonts form a nuptial cyst in which, under its protection, the amoeboid gametes from the two gamonts may mate.

gerontic (growth stage) – the ultimate growth stage distinguished from ephebic (adult) growth stages by a reduction in rates of growth and usually many structural irregularities.

global community maturation (GCM) - gradual change in the composition of a community by evolutionary and coevolutionary processes in a global ecological realm such as a climatic belt around the globe and any one of its subdivisions, such as the photic zone within the tropical oceans. The time period governing a GCM unit is of geological dimensions. Disrupting geological events which produce the boundaries of the larger chronostratigraphic units in the geological time scale often truncate the GCM cycles.

glomerulus – a nepiont characterized by streptospiral coiling (prior to fixation of a coiling axis) in fusulinids, alveolinids and many smaller imperforate foraminifera, often exclusively in the microspheric generation. Fig. 57.

Golgi body [Golgi apparatus] – a cell organelle consisting of a stack of flattened vacuolar cavities (cisternae). In the foraminiferal cell, the Golgi body produces the high-magnesium calcite needles which, after exocytosis, are used for bonding grains in the agglutinated shell or for the construction of porcelaneous walls. Fig. 56.

granular texture - see jagged granular and mosaic granular texture.

granule – see bead, papilla.

groove – an elongated depression produced by external local thinning of the outer lamella. It is deepened by persistent thinning ot the secondary laminations and a concurrent thickening of adjacent inflational costae or ridges that are usually present. The grooves reflect the flow of pseudopodial protoplasm extruding from interlocular spaces (feathering) or along the shell's periphery (cord). They my be covered or partially closed by secondary lamellation in later stages of growth and converted into canals. Fig. 50 & Fig. 64 A.

gutter - in Amphisteginidae: the free end of the stellar septulum, folded anteriorly at an angle to the axis of coiling. May be identical with the counterseptum in New World amphisteginids. Compare foramenal plate. Fig. 33.

H

hamulus - see tooth. This term has been coined for endothyrids.

haploid – having a reduced set (half of the total number) of chromosomes in the gamontic generation as compared to the full set (diploid) in the agamontic generation. Fig. 5.

hemiseptula - in Amphisteginidae: the infolds of the inner lamella partially subdividing a chamber. Fig. 58.

hemiseptular suture – the line of adherence of hemiseptula to a lateral wall.

hispid - covered with minute pustules or pseudospines.

holotype – see type.

homologous – equivalent morphological features of common evolutionary origin. May have different shapes and functions.

homomorphous - identical or similar in morphology but of different phylogenetic origin.

homonym – the same name for different taxa. Each taxon must have one name and one type.

host – an organism housing symbionts.

husband, **husbandry** - see chloroplast husbandry.

hypodermis - exoskeletal structures below an epiderm. See: polygonal network; alveoles.

hypodigm (Latin: hypodigma) – at a species level all specimens that a taxonomist considers to belong to that one unit. The hypodigm also includes the specimens of previous workers as listed in the synonymy. See also type.

I

imperforate - lacking pores or parapores.

incisional ornamentation - pattern of primarily thinned portions of outer lamella deepened by secondary thin lamination, usually adjacent to inflational ornaments. See also: grooves.

index of elongation - see elongation index.

indistinctly radial texture - appearance under crossed nicols of extinction in the center of a fragment of test with other extinctions irregularly distributed. Corresponds to a bundle-shaped ultrastructure.

inflational ornamentation – a pattern of primarily thickened, often imperforate areas of outer lamella becoming additionally thickened by secondary lamination. See also: pustules; beadings; pseudospines; costae; carina.

inflational pillar - see pile of lamellae.

inframarginal sulcus - see infundibulum.

infundibulum [inframarginal sulcus] (scrobis septalis, pars auct.) – a distinct proximally directed infold in a distal chamber wall located beneath the periphery on the umbilical side of trochospiral forms. See also: marginal prolongation. Fig. 61.

inner lamella (inner lining, inner calcareous layer, pars auct.) - the inner mineralized part of the primary bilamellar chamber wall between an inner organic lining and a primary organic sheet. Made up mainly of stacked calcitic platelets or of aragonitic prisms. In calcitic foraminifera it comprises also the inner array of large, paired rhombic crystals formed initially on both sides of the primary organic sheet, crystals that some authors include in the so-called median layer. Fig. 75.

inner organic lining (IOL) - see organic lining. Fig. 75.

instar - a single step in the discontinuous growth process of most foraminifera. It is reflected by the formation of one chamber of the shell (or of a cycle of chamberlets). See also: chamber; chamberlet cycle; lamellation.
Remarks: The use of this term in foraminiferology is contested, mainly by biologists. The *Cambridge Dictionary of Biology* (**WALKER** P.M.B., ed., 1990) defines instar as "the form assumed by an insect during a particular (ontogenic) stadium" (such as pupa, imago etc.). Others have used the term for the period of existence of marine arthropods between moults (ecdysis). Transferred to foraminifera, the formal definition would mean the stages of growth commonly designated as embryonic, nepionic or ephebic, each characterized by the addition of several or numerous chambers. However, because in foraminifera each growth-step modifyes the form of the shell and can be individually identified in every specimen by counting the number of chambers, I see no reason to reject the already traditional and most convenient use of this term as substitute for growth-step. Thus, an instar of a lamellar foraminifer includes whatever the shell produces by the same growth-step, *i.e.* the walls of the a chamber or of a chamberlet cycle and the respective outer lamella that covers all the exposed surfaces of the previous shell and participates in the construction of surficial ornements including piles, umbilical plugs and umbos. See also: supplemental skeleton, where the distinction of successive growth-steps is difficult.

interauxiliary chamber(s) - periembryonic chambers that lack direct communication with the embryo lumen. They form the periembryonic spirals in miogypsinids.

intercameral foramen - see foramen.

interio-areal aperture - aperture situated near the base of the distal wall, but not at the suture with the preceding coil. See also: aperture.

interiomarginal aperture - aperture situated at suture between the distal wall and preceding coil.

interlamellar organic sheets - sheets of organic material occurring between consecutive secondary outer lamellae. Fig. 75 C.

interlamellar space – a space formed between successive outer lamellas or by flying covers of primary, bilamellar walls. These spaces may be inflated to become a supplemental chamberlet, fed by canal orifices, not by apertures nor stolons, and hence are independent of the arrangement of primary chambers. Seen in particular in *Siderolites*, *Pellatispira* and consorts. See also: supplemental skeleton. Fig. 65.

interlocular space (lacuna, pars auct.) - a space formed as a consequence of a deeply sunken suture between consecutive chamber walls or between consecutive coils. See: intraseptal and spiral interlocular spaces. Fig. 26 A.

interpore ridges - the external residual or built-up test material in the areas between large pores. Fig. 28.

interradius (pl. interadii) - in orbitoidiform architecture: sector of undifferentiated equatorial layer inbetween radii.

interseptal - located between consecutive septa.

interseptum (in Amphisteginids for instance) – the partial subdivision of a spiral chamber by infolds of the inner lamella in a direction that is more or less parallel to the septum.
Remarks: The term is impropriate. Structural elements subdividing spiral chambers in lamellar shells are septula, not septa. Use instead hemiseptulum.

interseptal pillars [pillars] (lamelliform buttresses) - in porcelaneous and agglutinated species: the multiple columnar projections between consecutive septa and parallel to protoplasmic flow. Pillars are part of the endoskeleton. To be distinguished from piles of lamellae. Fig. 47 E-G & Fig. 72.

intradermal plate - see beam; septulum. In order to avoid ambiguity tis term should not be used.

intraseptal interlocular space - the interlocular space formed between the posterior bilamellar wall of a chamber and the distal bilamellar wall of the preceding chamber, as a result of a deeply sunken suture. Intraseptal spaces may be open to the exterior along their margins either continuously or through openings between points of marginal adherence of consecutive lateral chamber walls. See also: sutural canals; fossettes. Fig. 44.

intraseptular space - space formed in the wall (septulum) between adjacent subsidiary chamberlets of the same instar, produced by lateral infolding of the chamber wall. May contain canals communicating with an intraseptal canal system.

intrathalamous - situated inside the test.

intraumbilical - see umbilical.

involute chamber arrangement - in spirally coiled forms where - due to chamber shape - the lumina of the chambers in one coil cover laterally those of the preceding coil. See also alar prolongations. Fig. 7.

isodiscodine - see biconch.

J

jagged-granular texture - appearance under crossed nicols of a fragment of the test wall showing minutely granulated crystals with irregularly shaped sutures. The crystals usually have a more or less uniform yellowish colour in polarized light. This texture indicates an intricate ultrastructure.

joist - see beam.

juvenarium - see nepiont.

K

keel – see carina.

keriotheca – an alveolar, honeycomblike structure of the spirotheca in advanced fusulinids, consisting of an "upper", extern and a "lower" intern "layer" produced by a split of the alveoli into narrower subunits below a tectum. Fig. 62.
Remarks: The terms "upper" and "lower" layer of keriothecal structures refer to the traditional orientation of single chambers or wall parts in specialized papers. They should be replaced by the terms **extern** and **intern** when referring to their position within the shell, quite independently of the orientation of the illustrations.
The term "keriotheca" is restricted here to structures with two layers of alveoles. Alveolar layers with uniform radial elements, as in Verbeekinid fusulinids, must have another designation in view of the importance of these strucural differences in higher systematics (see pseudokeriotheca, parakeriotheca).

knob - see boss, umbo.

L

labial aperture - see foliar aperture.

labyrinthic – a spacial disposition of subdivided chamber cavities without regularity or pattern. In most cases however, the labyrinthic disposition is only apparent, in one instance due to the strong curvatures of consecutive septa in both axial and equatorial directions, so intersections with structural elements in oriented sections of the shell are oblique, as in spiral *Anchispirocyclina*.

lamellation – a mode of wall formation by extracellular biomineralization on organic sheets (templates) shaped - for the chamber under construction - by temporary ectoplasmic strands similar to brush borders of other cells. The external organic coat of previously formed, exposed hardparts may form an additional template for the deposit of an outer lamella. In his monograph on rotaliids, **SMOUT** (1954) formulated for the first time this very basic principle of wall formation that was subsequently refined and modified by **HANSEN** (1999).

lamellar wall – a test-wall consisting of layers of calcite or aragonite formed at consecutive instars and covering the exposed surfaces of the test already formed. This wall generally possesses true pores produced in consecutive lamellae by so-called blueprints. Most lamellar genera are bilamellar and some primarily multilamellar.

lamelliform buttress - see beam if exoskeletal, septulum or pillar if endoskeletal.
Remarks: **HENSON** (1948) introduced this term for chamber partitions leaning against free outer (mostly lateral) walls as suggested by the meaning of the term in architecture. Buttress is by and large a synonym for subepidermal partition. **HOTTINGER** (1967) showed the distinction of endo- and exoskeletal structural elements to be of taxonomic and phylogenetic relevance and defined terms that are specific to each category of partitions. There is no reason to continue the use of the term buttress. Where a neutral and purely descriptive term may be helpful in a case difficult to interpret, it is sufficient to speak about "partitions".

lamination [secondary lamination] - layering of test-walls due to superposition of consecutively deposited outer lamellae on exposed outer shell surface. See also: lamellar wall.

lateral canals - see sutural canals.

lateral chamber wall – that portion of the main chamber wall never converted into part of a septum; more or less clearly separated from the chamber periphery or peripheral wall.

lateral chamberlets (cubicula) - in orbitoidiform architecture: chamberlets of roughly isometric or irregular to vermicular outline, layer-wise arranged in a chessboard pattern. They cover both lateral surfaces of orbitoidiform shells. Retral stolons connect the main chamberlets in the median chamberlet layer with the adjacent lateral layers of chamberlets. Consecutive layers of lateral chamberlets are connected with oblique stolons. The lateral

chamberlets of one layer may be connected between themselves by more or less restricted passages. There may be gradual transitions between lateral chamberlet layers and expanse chambers.

lateral openings – a gap for intracameral communication in neoschwagerinid septula, at the junction of exoskeleton and endoskeleton and hence homologous to the lateral annular passages in anchispirocyclinids. See also: passage.

latero-marginal aperture – a primary aperture situated on a lateral umbilical wall of coiled tests, in a subperipheral position.

life cycle - most eucariotic, free-living cells reproduce asexually but shift from time to time to sexual reproduction in order to avoid degeneration (**MULLER**'s ratchet, 1964). In many foraminifera the alternation of sexually and asexually produced generations is documented in the morphology of the shell by dimorphism or trimorphism (see: gamont, schizont, megalospheric generation, agamont and microspheric generation). In foraminifera, there are many different types of life-cycles (**LEE** *et alii*, 1991; **GOLDSTEIN**, 1999). They differ in particular by the position of the nuclear reduction division (abbreviated R!) within the cycle. Planktic foraminifera are interpreted as reproducing exclusively by sexual processes. See also: alternation of generations. Fig. 5.

limbate – a descriptive term for the thickened, more or less prominent sutures on the test surface at the boundaries of chambers. Fig. 77 F.

lip [apertural lip] – an everted, in lamellar forms imperforate extension of the chamber wall along an elongate cameral aperture. May be narrow or broad, small or large. See also: phialine lip; rim. Compare: folium.

loculus - chamber.

loop-hole – a small connection between chamber lumen and interlocular space. May be located at the periphery (leading into a sulcus in nummulitids), at the base of the chamber, as in elphidiids, or in front or in back of umbilical plates or cover plates, as in rotaliids. Fig. 34.
Remarks: The "septal passage" of **PARVATI** (1971) is a loop-hole in pre- or post-septal position. As the term "passage" is now reserved for connections between cavities of the same chamber (or instar), the term "septal passage" leads to confusion and is replaced here by pre- or post-septal loop-hole. Loop-holes function as backdoors for the extrusion of ectoplasm when the chamberplasm retracts to inner chambers during a perturbation in the ambient environment.

lumen - see chamber (or chamberlet) lumen.

M

maerl - coarse-grained sediment consisting of shells, coral fragments and other skeletal debris, that form extensive carpets on the sea floor where the components are bound by living algal filaments and/or coralline red algal crusts, and consequently resist erosion by rapid bottom currents. May be inhabited by normally epiphytic larger foraminifera.

main chamber lumen – a complete or segmented chamber cavity communicating with the preceding and succeeding main chamber lumina through primary or secondary intercameral foramina. In certain lamellar foraminifera the main lumina are separated partly or completely from a foliar or stellar chamberlet, as well as from canal systems by a foramenal plate, toothplate, umbilical plate, cover plate, or sealing plate.

main chamber wall – that portion of the walls of a test enclosing a main chamber lumen.

main chamberlet layer - in orbitoidiform architecture: cycles of chamberlets in the median (equatorial) plane of the shell, commonly annular, that are distinguished from a lateral chamberlet layer (if present) by their smaller size and more regular structure. A flange in orbitoidiform shells exhibits the

peripheral parts of a main chamberlet layer that lacks the cover of lateral chamberlets. The last cycle of main chamberlets bears the apertural face of the shell. Fig. 52.

main partition - in *Orbitolina*: (radial) septulum.

marginal apertures – a single row of apertures on the shell margin, distinguishable from areal multiple apertures by their oblique-radial direction, as in Tertiary conical agglutinated forms or in *Marginopora*. Single marginal apertures in lamellar-perforates, as in almaenids, may be closed by a secondary lamellation already present in the penultimate chamber.

marginal canal system - enveloping canals grouped at the periphery of the shell, often extended in radial direction, as in *Pseudosiderolites*, in contrast to cords, where the peripheral orientation of the canals is emphasized. Fig. 65.
Remarks: **HOTTINGER** (1978) used this term as a synonym of marginal cord. It seems preferable now to distinguish between predominantly radial and peripheral systems. The latter are never modified to include canaliculate spines. See also crest.

marginal chamberlet - see fistulose chamberlet.

marginal cord – a thickened shell margin produced by a peripheral system of numerous longitudinal anastomosing grooves and adjacent imperforate elongated ridges and islands of an inflational ornament type. Grooves are closed by secondary lamination and converted to an anastomosing bundle of peripheral tubular canals. The marginal cord is the diagnostic feature of the family Nummulitidae. Fig. 64.

marginal crest – the thickened shell margin produced by a marginal canal sytem, as in *Pellatispira*. It may be overgrown by supplemental chamberlets either on the lateral flanks alone (*Biplanispira*) or on all sides of the shell (*Vacuolispira*). Fig. 65.

marginal prolongation (tectum) - in a trochospiral test, a distally directed prolongation of the spiro-marginal portion of a chamber, leading the spiral sutures to be much more inclined on the spiral side than on the umbilical one. Fig. 61.
Remarks: This feature has also been called tectum, a term preoccupied in fusulinids by the outermost layer of the chamber wall in the chamber roof. Therefore the term tectum is not acceptable as an alternative to "marginal prolongation".

marginal trough – a circular depression between the marginal and central part of the chamber face in uniserial-conical foraminifera; it may be the site of a circular row of marginal apertures.

marginal ridge – a circular ridge in the discoidal chamber produced by a marginal trough, that marks the boundary between the marginal and the central chamber lumen, and often the limit between exo- and endoskeletal elements of the shell.

marginal zone – the marginal portion of the discoidal chamber in conical shells or of the lateral parts of an annular chamber in discoidal-evolute shells. It often houses an exoskeleton. In uniserial-conical shells the marginal zone is usually separated from a central area of the chamber by a furrow, the trough. The furrow is produced by a recess of the marginal zone for third or half of the chamber height (in the direction of growth). In discoidal-annular shells, a similar recess produces a pair of circular marginal troughs framing the apertural face, as in *Marginopora*. See also radial zone, reticular zone. Fig. 20 & Fig. 71 G.

marginoporid structure – a three-dimensional arrangement of endoskeletal elements as in extant *Marginopora*: apertural axes oblique with respect to radial direction, overcrossing in neighbouring stolon planes and alternating in radial position from one stolon plane to the next. Endoskeleton may consist of septula or pillars.

mask - mineralized element(s) of the test that obstruct a primary cameral aperture; resorbed in subsequent growth stages. Fig. 77 B.

maturo-evolute – planispiral-involute shells tending to become evolute in mature growth stages.
Remarks: Term introduced by **BANNER** and **HODGKINSON** (1991), exemplified by *Heterostegina depressa*. However, in that species and many other nummulitids, the degree of involuteness changes in relation to the depth at which the individual lived. Microspheric specimens tend toward maturo-evoluteness because their ontogeny is much longer than that of the permanently involute megalospheric generation of the same species. See also: evolute and involute in lamellar-perforate foraminifera. Fig. 7.

meandrine – a tortuous, winding path of linear features, in particular the septal sutures of long alar prolongations or supplemental chambers, as in some advanced agamonts of nummulitids, miscellaneids, meandropsines and archaiasines.

median layer - in bilamellar foraminifera a term applied to both the spongy primary organic sheet and the distinctly larger crystals formed initially in vesicles and occurring as pairs on either side of the primary organic sheet. See also: outer lamella; inner lamella. Fig. 75 A.

median section – a slice in the central sagittal position normal to the axis of coiling.

megalosphere – the large proloculus in di- or trimorphic species; a defining characteristic for gamonts and schizonts in contrast to the microsphere of the agamont. See also: alternation of generations. Fig. 5.

megalospheric - in dimorphic species: test having a large proloculus or megalosphere; commonly a gamont or schizont.

meiosis [reduction division] – step in the process of cell division, during which the chromosomes of the parent cell are reduced from a double to a simple set (from diploid to haploid) for each daughter cell. See reproduction cycle: Fig. 5.

metabolism – The sum of biochemical activity in a living organism. In perforate foraminifera the degree of its magnitude may be reflected to some extent by the diameter and density of pores in the shell walls in relation to the volume of the chamber lumina.

microgranular – a wall texture: under the optical microscope a granular appearence of walls composed of calcareous elements. More stable and resistant to diagenetic recrystallization than porcelaneous walls. In fusulinids and pfenderinids, the microgranular wall never encases agglutinated grains. In Mesozoic imperforates, agglutinated textures may be replaced by microgranular material if no grains are available in the ambient environment.

microsphere – the small proloculus of the agamont in di- or trimorphic species, in contrast to the megalosphere of the gamonts and schizonts. Microspheres never have multiple apertures nor structural complications. See also: alternation of generations.

microspheric - in dimorphic species: a test having a small proloculus or microsphere; commonly an agamont.

microstriae - minute longitudinal, usually anastomosing ridges on the surface of porcelaneous test. Most are visible only under high magnification, especially by Scanning Electron Microscopy. SEM.

microtubule - polymerized heterodimers of alpha and beta tubulin in helicoids that form long, straight cylinders reinforcing the pseudopodial ectoplasm of the pseudopods and the plasmatic content of interlocular spaces, *i.e.* canal systems. May depolymerize and form paracrystals in the chamber plasm. The paracrystals are believed to be the reservoir that feeds the polymerization when pseudopods expand through an orifice into the ambient environment. Fig. 67.

milioline - the taxa or the characteristics of the suborder Miliolina.

milioline coiling - in porcelaneous foraminifera: bilocular coils where all terminal apertures are positioned on one common axis (apertural axis). The axis of coiling is normal to the apertural axis and is rotated so that several descrete angles exist between the median planes of consecutive chambers:

these are 72° (quinqueloculine), 120° (triloculine) or 180° (spiroloculine or biloculine). If the chambers are positioned so that in a section normal to the apertural axis they form an S-shaped curve, their arrangement is called sigmoiline. See also: streptospiral. Fig. 37.14-17 & Fig. 68.

milioline tooth/teeth - one or more inward projections of the inner portion of the chamber-wall into the aperture of milioline species. May be bar-like, spatulate, bifid, or anvil-, T-, Y-, anchor-, spur-, scoop- or spoon-shaped. A single tooth is always present primarily in an interiomarginal position; it may be accompanied by additional teeth that project from the opposite margin of the aperture, from the chamber roof or from the lateral wall. See also: trematophore.

mitochondrion – the cytoplasmic organelle of a cell delimited by an outer membrane and enveloping a folded inner membrane (cristae); it is responsible mainly for the respiration of the cell. In oxygen-depleted environments, the foraminiferal mitochondria may assemble below the inner pore mouths thus documenting the role of foraminiferal pores in the exchange of small molecules with the ambient environment. Fig. 75 B.

mitosis – the "normal" cell division, where each daughter cell inherits the gamut of the chromosomes of the the parent cell.

monolamellar – a perforate wall consisting of one lamina, the outer lamella only, lacking both a median layer and an inner lamella. The outer lamella may cover the exposed parts of earlier formed shell completely or partially.

monothalamous [unilocular] – a shell consisting of a single chamber.

mosaic granular texture - under crossed nicols fragments of the test wall are shown to be composed of large sutured calcite crystals with finely serrated margins. Corresponds to clumpy ultrastructure.

multiple spirals – Plani- and trochospiral shells may produce supplementary spirals growing at the same rhythm as the primary spirals, in nummulitids indicated by simultaneous deviation from mean volume accretion rates during ontogeny. These deviations are interpreted as seasonal effects. Multiple spirals are known in alveolinids (*Multispirina*), possibly in meandropsinids (*Fallotia*), in nummulitids and in rotaliids (*Dictyokathina*, *Dictyoconoides*). Fig. 55.

murica – see pseudospine.

murus reflectus - see umbilical plate.

N

neanic – a postnepionic growth stage with the architecture of an adult shell. May be either a synonym for the adult or ephebic growth stage or designate an early phase of the adult stage. Should be used only where there is a qualitative delimitation to later adult stages, for instance the transition from spiral to flabellar or from flabellar to annular growth. Fig. 37.

neck – a tubiform extension in terminal position of the aperture, as in uvigerinids.

nepionic – the juvenile stage immediately after an embryonic and preceding an ephebic stage.

nepionic acceleration – the reduction of nepionic chambers in geologic time within a phyletic line of genera with either a spiral or a radial architecture.

nepiont – the growth-stage following the embryonic stage and different in architecture from the adult stage.

nonlamellar - chamber walls lacking a lamellar texture, as in most agglutinating and porcelaneous forms.

notch (French: encoche) – a single indentation of the proximal chamber wall in a sutural position. It marks the limit between a spiral main chamber and its folium and may extend into an internal infold. See also: foramenal plate. Fig. 34.

nucleoconch - see embryonic apparatus.

nucleus - the cell organelle that contains the genomic material organized in chromosomes and that is bounded by a double membrane. In foraminifera, a single, larger somatic nucleus that may be polyploid controls the metabolism of the cell. It degenerates when, at the start of the meiotic process, several smaller, generative nuclei divide prior to reproduction.

O

oblique section – a slice through a test cut neither parallel nor normal to its axis. It may be centered, that is show the proloculus, or noncentered. Fig. 83.

odd pairs or **associations** (Français: associations dépariées) - common associations of two or more foraminiferal species that exhibit an identical or a closely related architecture in their adult form but differ markedly in their adult size. In most cases, the difference in the size of the adults is matched by a corresponding, size-dependant architecture in the megalospheric embryo, *i.e.* a large embryonal apparatus in the larger form, versus a simple, more or less undifferentiated megalosphere in the odd partner. These partnerships are usually restricted to one or two pairings of species. An example of a recent odd pair is the frequent association of *Amphisorus hemprichii* with the odd partner *Sorites orbiculus*. They have the same habitat on seagrass leaves but reproduce at different times in the seasonal cycle (**HOTTINGER**, 1999). An example of a fossil odd pair is given in Fig. 70.

odd partner - the smaller representative of an odd association.

oral - apertural. See: aperture, foramen.

orbitoid(al) architecture – an arrangement of chambers like those of in orbitoids s.l., *i.e.* an annular series of chamberlets form a sagittal, equatorial main chamberlet layer covered on both lateral surfaces by corresponding cycles of lateral chamberlets or expanse chambers.

orbitoid(al) growth – an arrangement of chambers like those of orbitoids s.l.: a layer of annular chamberlets alternating in radial position in successive cycles, each chamberlet communicating in a diagonal direction with its neighbour in the previous and following annuli. Fig. 36.

orbitolinid structure – an arrangement of endoskeletal and exoskeletal elements in space like that of *Orbitolina* and some of its closest relatives; *i.e.* a radial subdivision of the discoidal chambers by septula that fuse with an exoskeletal polygonal network, where the septula adjust to radial rows of apertures with crosswise oblique stolon axes. Fig. 71.

orbitolitid structure – an arrangement of endoskeletal elements as in *Orbitolites*: apertural axes oblique in respect to the radial direction in the discoidal shell, overcrossing and superposed in radial positions in neighbouring stolon planes. So far, only septular (*i.e.* continuous) endoskeletal elements are known to follow the orbitolitid pattern of stolon axes. Orbitolinid structure is basically the same as orbitolitid structure, but it produces radial subdivisions within a discoidal chamber whereas the orbitolitid structure produces subdivsions of an annular chamber. Fig. 47 H.

orbitopsellid structure - arrangement of endoskeletal elements as in *Orbitopsella*: the arrangement of endoskeletal pillars follows the pattern of the radial stolon axes that alternate in radial position from one stolon plane to the next. Exoskeletal elements consist of beams only. Fig. 72.

organic lining – an organic cell envelope said to consist of mucopolysaccharides, located between the plasmalemma and the biomineralized cell envelope. It covers the protoplasmic cell body in the chamber lumina and the connecting cavities inbetween them (foramina, stolons), but never the interlocular spaces. Whether it occurs in chamberlet cavities of the supplemental skeleton is unknown at present. May be discontinuous or extremly thin

over pore mouths and/or in the ultimate and penultimate chambers, and commonly thickens in the direction of earlier growth stages. May be involved in stolon plugging. May be resorbed together with the biomineralized wall when brood chambers are formed. The organic lining resists dissolution of the biomineralized shell by acidic attack, maintains the shape of the protoplasmic body and is capable of remineralizing its shell when the ambient environment returns to normal. However, the role of the organic lining in biomineralization has to be investigated further. Fig. 69 & Fig. 75 .
Remarks: There is no reason to abandon the traditional designation of organic lining (as used by **LOEBLICH** & **TAPPAN**, 1987) in favour of "inner organic lining" (IOL) as introduced by **ANDERSON** and **BÉ** (1978). The eventual use of an "outer organic layer" called for by the IOL that might be applied either to the outer organic cover of the biomineralized shell or to the temporary organic envelope that in some species protects the process of chamber formation would add confusion in the description of the several layers of the cell envelope and their specific functions. Moreover, the term "inner organic lining" is easily confused with the term "inner lining" which is equivalent to "inner lamella", the inner calcified lamella of the primary wall in perforate foraminifera.

organelle – a morphologically distinct, named unit in the cell plasm, usually visible in the transmission electron microscope. It performs one or several, well defined functions. See in particular: nucleus, mitochondria, Golgi apparatus, chloroplast, vacuoles, rhizopodia.

orifice – any unspecified opening in the test such as apertures or the mouths of a canal system. The term is to be restricted to a functional meaning, *i.e.* to those openings where protoplasm extrudes from the shell.

ornamentation – the patterns formed at the shell surface that are generated by a regular modification of wall textures (perforation, pitting), of the thickness of outer portions of the wall that generates ribs, beads, papillae, pustules, pseudospines, etc., or of a combination of both. See also: inflational ornamentation; incisional ornamentation; textural ornamentation.

outer lamella – the mineralized layer of the primary wall in bilamellar foraminifera, on the outer side of the primary organic sheet. At its contact with the primary organic sheet is the outer array of distinctly larger paired crystals (included by some authors in the so-called median layer) succeeded by the stacks of calcite platelets or pseudohexagonal aragonite prisms that form the major part of the outer lamella, and is completed by the outermost thin layer of blocky columnar crystals that comprise the veneer. Fig. 44 & Fig. 75 A .

P

papilla [pl. papillae] – a small, rounded, poorly or non-perforate protuberance, single or multiple, on the outer surface of perforate chamber or chamberlet walls, produced by local inflation of outer lamellae and linked to a conical outward spreading of the pores. Fig. 73 .

parachomata - chomata that supplement the primary pair of ridges in the equatorial zone of the shell laterally polewards; regularly intercalated between supplementary tunnels up to the polar end of the chamber as in *Pseudodoliolina*. May fuse with the beams of an exoskeleton in order to form complete partitions in the chamber, as in neoschwagerinids. Fig. 74 .

parafossette – an opening between bifurcating ponticuli and the margin of the preceding chamber wall. They communicate with intraseptal interlocular spaces and fossettes. Fig. 54 .

parakeriotheca – a single layer of uniform, radial, closely spaced and more or less parallel cavities in the spirotheca of advanced fusulinids, covered by a tectum.
Remarks: This term is introduced here to emphasize the significance of the difference between one- and two-layered keriothecas. The single layer is interpreted as a wall texture similar to pores and parapores, lacking a plasmatic filling and serving to facilitate gas exchange through the shell. The interpretation of the "alveoles" as pore-like textural elements derives from their similarities to the construction of pores: like the lamellar constructions in perforate foraminifera, the chomatopores are constructed by replicating the pore cavity from one layer to the next without morphogenetic intervention by the protoplast.

parapores (canaliculi; pseudopores, pars auct.) - in agglutinated foraminifera: straight to tortuous tubular spaces, round to polygonal in section, more or less normal to the test surface, coated and closed off internally by the organic lining. May be branching and anastomosing and - usually - restricted to the inner wall-layer, thus ending blindly beneath an outer solid "pavement". No sieve-plate present. Parapores may be laterally interconnected. They may lead into irregular cavities or fistulose chamberlets between a paraporous wall-layer and the pavement. The partition between a main chamber lumen and a fistulose chamberlet, wherever present, is always paraporous. Compare: pores; pits. Fig. 6 & Fig. 51 E.

paries proximus – an integrative term designating the proximal, septal chamber wall and the various extensions produced independently by the inner lamella at the bottom of the chamber or at its adaxial umbilical region, including also structures in the previous chamber such as umbilical cover plates.
Remarks: this term was introduced by **LÉVY** *et alii* (1979, p. 68) in order to support the revision of discorbid foraminifera. It integrates the following terms currently in use: septal flap, proximal wall, foramenal plate, abaxial cover plate and umbilical plate. It is a partial equivalent of **HOFKER**'s (1951) toothplate. This term also is too broad to be helpful in distinguishing the various structures that are diagnostic for defining the genera in several families. **HOFKER**'s idea (1956) was to place all ("tooth"-) plate-bearing taxa into a common group, the "foraminifera dentata". Despite this, the paper of **LÉVY** *et alii* (1979) is most important for it constitutes the basis of **LOEBLICH** and **TAPPAN**'s conception of the Discorbidae (1987) in present-day systematics.

partitional pore(s) - see passage(s).

passage – the means of communication between adjacent compartments of the same chamber; it is an opening that may be sited below the frontal chamber wall (preseptal), after the septal wall (postseptal) as in alveolinids, or at the fusion between exoskeleton and endoskeleton, as in verbeekinids. In peneropliform to concentric architectures, the passages may be semiannular-annular, in a preseptal position, as in *Sorites*, or paired in lateral positions, separating exoskeleton from endoskeleton, as in *Anchispirocyclina* or *Orbitopsella*. Fig. 72 & Fig. 79.

pavement - in agglutinated foraminifera the outer layer of solid wall covering an inner paraporous layer. Fig. 51.

penultimate chamber - chamber before the last in an individual.

perforate - referring usually to walls possessing true pores. Where the term is applied to walls possessing parapores it should be replaced by "paraporous".

perforation pattern – the pattern of distribution of external pore mouths on lamellar shell surfaces, either combined with or totally apart from the ornamental sculptures of the shell.

periapertural depression - see adapertural depression.

periembryonic chamberlets [corona] (periembryonic cells) - all chamberlets in contact with an embryonic apparatus. In orbitoidiform architecture the term is restricted to the chamberlets of the equatorial main layer and is a synonym of "corona". In orbitolinids the periembryonic chamberlets designate the forth stage of growth consisting of an annular chamber subdivided into chamberlets. The fifth chamber may be called nepionic, and is annular or discoidal, radially subdivided by septula following the constraints of crosswise-oblique stolon axes disposed in radial rows. Fig. 41 I-L.
Remarks: Introduced by **DOUGLAS** (1960), the term periembryonic originally included subembryonic chambers, without analyzing in detail the complicated structures of this part of the test. Today, much weight is given to the distinction between periembryonic and subembryonic chambers (**SCHROEDER**, 1962; **ARNAUD-VANNEAU**, 1980). See also: auxiliary chamber, adauxiliary chamberlets.

peripheral chamberlet - see fistulose chamberlet.

peristome [peristomal lip, peristomal rim] – a raised rim or tube around an aperture or foramen.

phenetic – morphological (in the context of evolutionary theory).

phialine lip - lip on apertural neck.

photoinhibition - diminishing rates of photosynthesis under stronger irradiation than necessary for optimal rates.

photosynthesis – reduction of carbondioxide to carbonhydrates powered by energy from solar irradiation absorbed by chlorophyll pigments.

phototropy – orientation of organism towards (positive phototropy) or away from (negative phototropy) sunlight by growth or active movement.

phrenotheca - thin, calcified partitions that divide chambers irregularly in various directions, as in *Pseudofusulina*.

pigeon-hole – an alveolar cavity in the exoskeletal polygonal network that expands at its blind end below the epiderm into a polygonal shape. Its opening into the chamber cavity is delimited by longer beams (perpendicular to the septum) and by shorter rafters (parallel to the septum). Fig. 45.

pile (inflational pillar, cristalline cone auct.) - superposed lamellar thickenings (pustules) on lateral walls or folia in consecutive whorls or consecutive chamberlet layers, that produce an aspect of pillar-like structures in the sections of shells. Compare: interseptal pillar. See also blueprinting.

pilintradermal plate - see beam.

pillar - see interseptal pillar. A pillar is not a pile!

pillar-pore - see calyx.

pioneering – an early stage of community maturation initiated in a totally or almost empty habitat invaded by immigrants specialized for rapidly occupying empty spaces with their unused resources. See also: community maturation.

pits (pseudopores; punctuations, pars. auct.) - in porcelaneous foraminifera, and in spirillinid and some unilocular genera: small cavities in the wall opening at the external surface of the shell, that are rounded to oval in section and tubular to conical in shape. They penetrate the shell surface at normal and oblique angles to depths that vary according genus. Sometimes they occur in several tiers and commonly anastomose thus resembling the parapores of agglutinating foraminifera but opening to the exterior. The term "pitted wall" is often used to describe the texture of the test of planktic, non-spinose foraminifera possessing distinct external pore-funnels or "pore-pits".

planispiral chamber arrangement – chambers arranged in whorls where the rate of translation (net rate of movement along the growth axis to the net rate of movement away from the axis) is zero. The spiral and umbilical sides of the test are identical and symmetrical with regard to the plane of bilateral symmetry. Fig. 37.1-3 & 5.

plastid – see chloroplast.

plastogamic plate – a plate-like structure covering the umbilicus in plastogamic specimens of some benthic foraminifera. Fig. 48 J.

plastogamy – two gamonts form a pair by joining their faces and exchanging gametes within a common shell lumen where fecundation takes place. Zygotes are hatched from the paired shells to form an agamont embryo. The mother shells are then discarded (see **ERSKIAN** & **LIPPS**, 1987). The faces of the shells are decorated by numerous rows of small pustules (costellae) in a radial pattern independent of the chamber arrangement. Fig. 48.

plate suture - line marking the trace of the adherence of the umbilical plate to the lateral chamber wall.

plectogyral - see streptospiral.

plesiotype – see type.

plug [umbilical plug] – an expanding pile of thickened lamellae in axial position in an umbilicus or in an umbilical bowl. May be single, compound and/or canaliculate. Fig. 77.

pole (of shell) - in subspherical to fusiform shells the point where the tips of involute chambers in a planispiral whorl meet the axis of coiling. Fig. 83. See also: polar torsion.

polarity (of chamber wall) – a textural differentiation of outer and inner portions in non-lamellar primary chamber walls. See also: agglutination, basal layer, flosculinisation.

polar torsion - helicoidal torsion of septa and septal sutures at the poles of fusiform larger foraminifera (mainly in fusulinids and elongate alveolinids), enforced by the broadening of the apertural face and usually linked to a polar multiplication of apertures.

polygonal subepidermal network - exoskeletal structure formed by a layer of always undivided, deep, tubular recesses in chamber walls, ending blindly below a thin, often transparent epiderm or similar structure. They generate a polygonal pattern at their distal end and open proximally into the chamber lumen with rounded mouths that are slightly restricted between lateral partitions of the chamber differentiated in beams and rafters. Fig. 47 E-G.

Remarks: In foraminifera with greatly inflated chambers like *Bradyina* or *Gyroconulina*, the beams may produce a polygonal pattern of their own rather than form a row of partitions perpendicular to the septum.

Introduced by **H. DOUVILLÉ** in 1906 under the name "réseau sous-épidermique", the term was used mainly in the description of orbitolinids where already in 1930 **DAVIES** distinguished major and minor partitions. In the later Anglosaxon literature, these details were not considered as important: **COX** (1937) described the *Loftusia* exoskeleton as "alveolar layer" and **HENSON** (1947) preferred to use the general term "subepidermal partition" for all elements subdividing the chamber lumen into "pidgeon-holes" or "subepidermal cells". The general term "subepidermal partition" was extended by **HENSON** himself and by later authors to any kind of lateral chamber partition, thus depriving the term of any significance for studies of comparative or functional anatomy. For this reason, we recommend dropping the use of the term "subepidermal partition". **HENSON**'s term "pigeon-holes" rather than "subepidermal cells" is appropriate to distinguish these from ordinary alveoles or alcoves.

A polygonal network has not been found in any living foraminifer. Therefore, that the recesses were coated by the organic lining can not be directly confirmed. The interpretation of the polygonal network as an exoskeletal structure rather than as a particular kind of wall texture (as **HENSON**, 1947, had already pointed out) is supported by their common combination: lamellar *Fabiania* and its relatives exhibit a perforate epiderm covering their subepidermal network, advanced *Cuneolina* and *Dicyclina* have a paraporous epiderm and many fusulinids bearing a parakeriotheca combine this wall texture with an exoskeleton. The extremely thin, often transparent epiderm in agglutinated foraminifera suggests, that the polygonal network is a device to keep symbionts exposed to light and in the immediate vicinity of the location where gas exchange through the shell should be enhanced by particular, porous textures.

It may be of taxonomical importance at a supra-generic level to distinguish at least two kinds of polygonal networks. The first one to appear in the Mesozoic (*Haurania* and *Amijiella*, Middle Lias) is comparatively coarse and deep. There is probably no clear differentiation of an epiderm, just a thin outer wall covering the polygonal ends of the blind recesses. The differentiation of beams and rafters does not seem to be very orderly, even in evolute, fan-shaped to discoidal shells such as *Timidonella* or *Alzonella*. The second group that appeared not much later with *Pseudocyclammina liasica*, has finer meshes and a clearly differentiated, extremely thin epiderm. This type characterizes most late Mesozoic conical foraminifera as well as the peneropliform spirocyclinids.

The question arises: is there an evolutionary series of exoskeletonal development from simple to complex, such as *Praekurnubia* (Late Middle Jurassic) with simple beams as exoskeleton, through *Kurnubia* (Early Upper Jurassic) with a comparatively simple polygonal network, to *Rectokurnubia* (Late Upper Jurassic) with a deep and more complex polygonal network. Similar evolutionary trends have been proposed for reticulinellids and conical

agglutinated foraminifera. In the ontogeny of specimens belonging to one of the numerous genera involved no such series of exoskeletal structural complication has been observed. In my view, the question remains unresolved (for discussion see **HOTTINGER**, 1978, table 1, p. 255).

ponticulus, pl. ponticuli – a bridge of lateral wall spanning an intraseptal interlocular space. It may be massive or hollow. If hollow, it covers a retral chamber process. Compare: basal lobe; retral lobe; fossette. Fig. 54.

polythalamous (multithalamous, multilocular) – a shell consisting of numerous chambers.

polyvalent individuals (polyvalent tests, twins or triplets) - individuals with two or more megalospheric embryos belonging probably to the same clone, with a common late growth stage. Accidental association, not related to gamontogamy.

porcelaneous test wall - composed of optically cryptocrystalline lathes and rods or needles of calcite produced in Golgi vesicles within the protoplast and transported through the cell wall by exocytosis to the site of wall construction. Rods arranged randomly, lathes arranged in a tile-roof pattern and forming the outer wall-layer. Wall imperforate, but may possess pits.

pore – a minute tubular perforation traversing a lamellar chamber wall, coated internally by an organic sheathe. Subdivided by organic discs ("pore plate" auct.) and closed off internally by the inner organic lining. The latter may fuse with the basal disc corresponding to the median layer and form an organic pore plug. The size and shape of the external and internal pore openings may be identical (rounded to elongated) or dissimilar, when symbionts are positioned in egg-holders below the pore mouths for gas exchange. Ultrathinsections of living benthic foraminifera that show in the TEM some cytoplasm in pores are considered to be artefacts due to imperfect preparation. Compare: parapores; pits. Fig. 75

pore-chimney – an enlarged pore-cavity in a secondarily laminated wall, grouping 2-4 smaller pores of the primary chamber wall. 178/5,7.

pore-fields - local concentrations of pores in certain areas on the surface of the chamber wall. Fig. 75 F-G.

pore-funnel [pore-pit] – the externally enlarged outlet of a pore (in planktic foraminifera).

pore-pit – see pore-funnel.

pore plate [pore sieve-plate] – a minute, microperforated, more or less calcified disk located in the pore tubulus at the level of a distinct constriction which reflects the position of the primary organic sheet (median layer). Fig. 75 A.

pore plug – an organic structure plugging a pore funnel. It is produced by the coalescence of the organic cell envelope and the organic median layer over the pore lumen. May be partially calcified by minutely perforated platelets called abaxialpore sieve plates. Fig. 75 A.

preseptal passage (preseptal canal, annular passage auct.) - in porcelaneous fusiform shells an elongate, undivided space beneath the septal wall containing the apertures. Fig. 79.

primary - belonging to the last formed, *i.e.* ultimate chamber.

primary aperture - see main cameral aperture; supplementary aperture; accessory aperture.

primary chamber - see chamber.

primary foramen - see aperture.

primary organic membrane (POM) - see primary organic sheet and median layer.
Remarks: This term (**BÉ** *et alii*, 1980; **ANDERSON** & **LEE**, 1991) is misleading and should not be used at all in foraminiferology for the following reasons: The median layer is part of an outer, biomineralized cell envelope and has nothing in common with the primary cell membrane (plasmalemma) of the foraminifer; neither their biochemistry nor their geometry are comparable (see **HOTTINGER** & **DREHER**, 1974; **LEUTENEGGER**, 1977). Moreover, the acronym POM is used in oceanography for "particulate organic matter" in the water column. Foraminiferal organic linings or its fragments are known to be one of many components of particulate organic matter, especially below the lysocline. The use of this term or its acronym may cause confusion.

primary organic sheet (primary organic membrane auct.) - sheet of spongy organic material between outer and inner lamellae in bilamellar foraminifera. In calcitic foraminifera, the primary organic sheet is usually bounded by rhombic, paired crystals which are different in size and shape from the stacks of platelets forming the major part of the mineralized layers. These crystals are interpreted as the nucleation sites for the biomineralization of both inner and outer primary lamellae on an organic template. Some authors include them in the so-called median layer.

primary plates - in orbitolinids: see exoskeleton. The term comprises beams and rafters.

primary spiral-umbilical canal – a more or less tubular or flattened space between the umbilical plates and the wall of the preceding coil or between plates, folia and the preceding coil; or between toothplates and the preceding coil. Fig. 26.

progenitor – a direct ancestor.

progressive chamber – a chamber with a supplementary, retrovert aperture giving rise to a supplementary series of chambers (in architectural types with multiple spirals or in orbitoidiform growth following the development of spiral nepionts.

proloculus – the initial chamber of a foraminiferal test without nepionic differentiation. Usually. a proloculus has a spherical outline and a single aperture.

protheca – the free chamber wall of fusulinids composed of a tectum and a diaphanotheca.

protoconch – the first chamber of a test with an embryonic apparatus or in which a deuteroconch is differentiated. In most dimorphic larger foraminifera, the microspheric generation has a proloculus, the megalospheric generation a protoconch or megalosphere. Fig. 41.

protoforamen – an aperture or intercameral foramen to which a toothplate is attatched.

protoplasm – the living matter comprising the cell-body.

protopore - comparatively narrow pores or parapores believed to represent early phylogenetic features.

proximal - nearer to the proloculus, contrary to the direction of growth.

proximal [posterior] **chamber wall** – the wall separating a chamber from the preceding one, formed by a septal flap or by a basal layer, or (in part) by a strongly inflected lateral wall that together with the distal wall of the preceding chamber produces an intraseptal space.

pseudalveolar - having a simple exoskeletal structure consisting of alcoves, as the agglutinated test of *Orbignya* or *Cubanina*.

pseudokeriotheca – a texture of external chamber walls in Mesozoic and later agglutinated foraminifers consisting of uniform, parallel, radial elements covered by some kind of tectum. The interpretation of these textural elements as pore-like cavities in the shell and their delimitation from the usually much larger and often more irregular parapores is not clear a present.

pseudoplanktic – a life habit: benthic forms emigrate into the planktic realm prior to reproduction, a strategy to enhance the dispersion of a population. Pseudoplanktic foraminifera produce as a penultimate growth step a float chamber followed by a balloon chamber with multiple apertures to release the hatching (Fig. 16). As fossils and in recent sediments, pseudoplanktic foraminiferal shells are found in comparatively small numbers disseminated over all the ecological gradients of the photic zone.

pseudopodia - semipermanent or temporary extrathalamous ectoplasmic projections. Foraminiferal pseudopodia form a reticular network (reticulopodia) reinforced by microtubuli.

pseudopore - see parapore, pit.

pseudorbitoid layer - see marginal canal system.

pseudospine (murica; spine, pars auct.) - a pointed conical, or elongated spine-like, usually solid but sometimes hollow, inflational ornament feature. Compare: spine; acicular spine; canaliculate spine.

pseudospinose - possessing pseudospines.

pseudoumbilicus (false umbilicus, pars.auct.) - externally visible, extra-axial, narrow or wide, cup-shaped space between an infolded distal wall below main cameral aperture and the adjacent coil, mimicking an umbilicus. Usually leads into an uncovered spiral umbilical canal. Compare: umbilicus; umbilical bowl; umbilical depression.

punctate (punctuation) - see pits.

pustule [tubercle; papilla] – a hemispherical to subconical inflational protuberance of the outer lamella. See also: pseudospine. Fig. 73 .

pycnotheca – in fusulinids: a uniform, dense part of the septal wall below the tectum, wedged between the keriotheca of two successive chambers.

pylome – see aperture.

pyrenoid – in foraminiferal symbionts a dense body rich in proteins in the chloroplast, often surrounded by storage carbohydrates (starch). Seen in the transmission electron microscope the shape of pyrenoids may be diagnostic for the differentiation of groups of algal endosymbionts. Fig. 30 .

Q

quinqueloculine - see milioline coiling.

R

radial – the direction from pole or axis toward any part of circumference of the test.

radial texture - see distinctly radial, indistinctly radial texture.

radial zone – the annular zone in the discoidal chambers of uniserial cones, where radial septula subdivide the chamber into radial compartments. See also marginal zone, reticular zone. Fig. 20 & Fig. 71 .

radiate aperture – a single aperture, in terminal or margino-terminal position with radially directed, slitlike or pointed extensions. The margins of radial apertures may fuse and thereby subdivide the aperture, as in many nodosariaceans.

radius (pl. radii) - in orbitoidiform architecture: a multiplication of the main chamberlet layer in four or five sectors of the equatorial plane (as in *Asterocyclina*) that produces star-shaped tests.

rafter – a minor exoskeletal partition of the chamber lumen parallel to the chamber septum and perpendicular to beams and the lateral chamber wall. Together with beams produces a subepidermal polygonal network. Fig. 47.
Remarks: The term rafter is a translation into English of **DOUVILLÉ**'s term "poutrelle" (1906) restricted here however to minor elements, the major ones being called "poutres" in French (or beams in English). **DOUVILLÉ** did not distinguish major and minor partitions in his "réseau polygonal" or polygonal subepidermal network at that time.

ramp – a linear surface in sections that traverse successive chambers with an endoskeleton defined by crosswise-oblique stolon axes. The ramp effect is produced by the stolons alternating their inclination in successive stolon planes of discoidal shells (*Orbitolites*) or cone mantels of uniserial cones (*Orbitolina*). Fig. 47 H & Fig. 71.

rectilinear chamber arrangement - chambers in a straight line.

reduction division - see meiosis.

regeneration – repair of the shell after injury, first by closing chamber cavities and subsequently by locally accelerated growth, until a specific outer shape of the shell is more or less perfectly restored. Shell fragments without an embryo may regenerate. This fact confirms that the nucleus of the cell moves away from the center of the shell during ontogeny. Fig. 78.

reniform - kidney-shaped.

residual pillar – an endoskeletal pillar supporting a frontal wall that spans a large preseptal space, frequent in trematophores. Where septula and floors are interrupted by a preseptal space, residual pillars may remain between (horizontal) preseptal passages and (vertical) shafts in support of the frontal chamber wall, as in elongate *Praealveolina*. Fig. 70 G & Fig. 82.

respiration – exchange of oxygen and carbon dioxide between an organism and its ambient environment.

reticular zone – the center of discoidal chambers in uniserial cones, where septula narrowing towards the center fuse into a reticular network in to minmize the volume of chamberlet cavities. See also marginal zone, radial zone. Fig. 20 & Fig. 71 G-H.

reticulate - having ornamental or other features arranged in a network. See: cancellate.

reticulopodia - see pseudopods, microtubules.

retral lobes - finger-like, hollow extensions of the proximal chamber-wall (in the absence of an interlocular space). See also: ponticuli; retral processes; basal lobes.

retral processes - finger-like proximally directed extensions of the chamber lumen covered by ponticuli present at the margins of an intraseptal interlocular space. Fig. 54.

retral [retrovert] **stolon** – in orbitoidiform foraminifera a stolon connecting main chamberlet lumina with lateral chamberlets. It is positioned in the median plane of the chamberlet parallel to the shell axis and is directed backwards, feeding the lateral chamberlets corresponding to its cycle. Fig. 36.

retroparies – see cover plate, umbilical cover plate.

retrovert foramen – a second, primary foramen located at the base of the marginal chamber suture, opening in a proximal direction and giving rise to orbitoidal growth after a spiral nepionic stage or to multiple spirals. Compare: supplementary apertures.

reversed trochoid chamber arrangement - trochospiral arrangement in which the spiral side more involute than the umbilical one.

rhizopodia - bifurcating and anastomosing pseudopodia, reinforced by microtubules.

rim [peristomal rim] – the thickened margin of an aperture. See also: lip.

S

saddle - the distally directed, u-shaped embayment between retral lobes.

sagittal section – a slice through the test normal to the axis of coiling and passing through the proloculus.

salients - rudiments of septa left over after the excavation of cuniculi (in fusulinids).

sarcode - see protoplasm.

schizont - apogamic offspring of an agamont reproducing either by another apogamous nuclear division and cytotomy (*i.e.* by distributing the mother protoplasm among the offspring) or undergoing meiosis. Because the foraminiferal schizonts are produced by cytotomy, they are megalospheric (A - forms). Fig. 5.

scrobis septalis - see infundibulum.

sealing plate (sealing-off plate; cover plate, pars auct.) - a thin plate, secondarily plugging the opening in an umbilical plate which - primarily - provides communication between a main chamber lumen and a foliar chamberlet. Never present in the ultimate chamber. Compare: cover plate.

secondary - belonging to the penultimate or to earlier chambers if they differ from the last one.

secondary apertures - see supplementary apertures.

secondary lamination - see lamination.

secondary passage - see interseptal, interlocular space.

secondary septum - see septulum.

secondary septulum - in neoschwagerinids: see rafter.

secondary spiral umbilical canal - tubular to flattened space comprized between cover plates and the lateral wall of the adjoining previous coil.

selliform – the deformation of a discoidal shell into a shape like a horse's saddel. Common in advanced *Discocyclina* ("*D. sella*") but also to be observed in *Orbitoides*, *Somalina* or *Eulepidina*. Selliform orbitoidal shells produce characteristic sections (Fig. 76). Whether this deformation is a specific taxonomic character or a functional response to bottom currents remains an open question.

septal face – that surface of a chamber-wall to be converted into a septum at a subsequent instar.

septal filaments - sutures of alar chamber extensions in involute nummulitids, often meandrine.

septal flap (paries proximus, pars auct.) – that part of the inner lamella that covers the preceding septal face. By its adherence to the septal face, the septal flap produces a trilamellar septum in a primarily bilamellar foraminifer. It may extend into an umbilical plate, a foramenal plate, a bipartitor, a cover plate or a toothplate. Fig. 53 F & Fig. 65 I-J.
Remarks: The term septal flap was used earlier for all parts of the proximal chamber wall, **LÉVY**'s paries proximus (**LÉVY** *et alii*, 1979). Here we restrict it to those areas of the proximal chamber wall that are glued to the face of the previous frontal chamber wall. This area may be minimized to a narrow hemicircular band around an interiomarginal foramen or reduced to sectors extending from the foramen over the face of the previous chamber either in equatorial or in dorsal direction. Free parts of the proximal chamber wall are covered by outer lamellas like all free outer surfaces of the lamellar shell. The open space between frontal and proximal walls of subsequent chambers is called intraseptal interlocular space. The line of adherence of the septal flap on the previous frontal chamber wall delimits the intraseptal interlocular space in proximal direction and is in fact a deeply sunken cameral suture.

septal fluting - see fluting.

septal foramen - see intercameral foramen.

septal passage - in rotaliids: provides communication between the main the chamber lumen and the spiral canal. See: loop-hole.

septal pore - primary small multiple apertures irregularly distributed on the apertural face (antetheca) of fusulinids. Fig. 66.

septal suture – the line of adherence of a chamber to the previous one.

septular suture – the line marking the position of a septulum below a lateral chamber wall.

septulum (French: cloisonette) - Endoskeletal, wall-like partition extending from the lateral wall into the chamber lumen, dividing it into compartments (chamberlets). In imperforate forms, these partitions are produced by local thickening of the inner part of the shell wall. Their disposition has a close relation to the arrangement of the foramenal axes. In lamellar-perforate species, the septula are produced by folded inner lamellas. Fig. 71.
Remarks: In describing alveolinid structures, there has never been any difficulty in distinguishing between a septum (closing off a chamber) and a septulum (partitioning the chamber into chamberlets) ever since **CARPENTER** (1862), **DOUVILLÉ** (1906) and **REICHEL** (1936-1937). In orbitolinids however, there is considerable confusion. **CARPENTER** (1862) described "*Patellina*" (= *Orbitolina*) *lenticularis* with a "large chamber layer". This term corresponds in modern terminology to a single, discoidal (or annular) chamber separated from the next "layer" by a septum. **R. SCHROEDER** kept up the idea of the chamber layer to at least 1973 but abandoned it in his 1975 paper. The concept of a chamber layer in orbitolinids leads to the interpretation of the orbitolinid radial partition as "septum" and of secondary, exoskeletal partitions as a "septulum" which is inconsistent with the structural interpretation of all other imperforate foraminifera. In French papers, where the orbitolinid mode of growth was correctly recognized as a uniserial stack of chambers, we find the simultaneous use of septum (for the true septum), cloison for endoskeletal radial main partitions and cloisonette (for beams in the exoskeleton).

septum (French: cloison) – a wall separating two consecutive main chamber lumina, *i.e.* the portion of the free chamber wall that is covered by subsequent chambers and thus incorporated in the architecture of the shell as a partition between successive main chamber lumina. The connection between them is assured by one or many openings in the septum (intercameral foramina, stolon systems) that are in most cases converted primary apertures. When multiple chamberlets form simultaneously the septum may consist of many discrete parts acting as partitions between the lumina of successive chamberlet cycles (not of neighbouring chamberlets).

sere (or series) – the complete sequence of biocoenoses in a succession, from pioneering stages to climax.

serial disposition of chambers (uniserial, biserial, triserial etc.) – the regular arrangement of a small number of chambers in a trochospiral shell that will produce one, two, three or more rows of chambers in a regularly superposed sequence in successive whorls. Fig. 37

sessile - permanently attached, usually with the attachment surface on the dorsal (spiral) side of trochospiral shells. Also designates a sedentary life habit.

shaft – a preseptal space vertically connecting superposed preseptal passages in elongate alveolinids. Fig. 70 G-H

sieve plate – a calcified disk with minute perforations closing the pore as a continuation of the median layer that separates primary inner and outer lamellas. Fig. 75 A.

sigmoid - s-shaped.

sigmoiline - see milioline coiling.

sinistral coiling - counterclockwise direction of coiling as viewed from the spiral side.

sipho - term broadly applied both to strongly folded buliminid toothplates and to entosolenian tubes.

six - stolon system – the manner in which each equatorial ogival or spatulate chamberlet of a main chamberlet layer is connected to its adjacent chamberlets, in the same cycle by annular passages and to the neighbouring two chamberlets in the following and in the previous cycle by crosswise oblique stolons. The pattern may be duplicated or multiplied in successive stolon planes parallel to the equatorial plane.

skeleton – all structural elements that supplement the primary chamber walls in shaping permanently the protoplast. The three basic skeleton types, endoskeleton, exoskeleton and supplemental skeleton may occur in all possible combinations that together with chamber shape and chamber arrangement determine the architecture of the shell. The term should not be used as a synonym of test or of shell both of which designate the total biomineralized cell envelope. Fig. 63.

socculus (pl. socculi) - in porcelaneous foraminifera low reliefs on the basal layer that do not touch the chamber roof. May form the pedestal-like base of pillars. On previous apertural faces, low ridges may connect neighbouring pillars or septula (*Amphisorus*). Ribs on basal layers may support pillars as in lacazinids. Socculi are a primarily internal feature of endoskeletal nature. They have to be distinguished from ornamental elements on the surface of chambers in previous whorls that have been covered by a chamber lumen of the next whorl, such as the plugs or ridges on the apertural face in *Amphistegina*.

sphaeroconch - in agglutinated larger foraminifera a spherical deuteroconch enveloping a thin-walled, often poorly calcified megalosphere. Usually possesses an exoskeleton, never an endoskeleton. Fig. 41.

spicular wall – a test composed of (secreted) fusiform calcite spicules.

spike - minute, conical to elongate spine-like projection on surfaces of the external wall of lamellar foraminifera, not thickened by secondary lamination. Spikes occur often on the walls deeply inside interlocular spaces, as in the fossettes of larger elphidiids, to fend off larger particles such as diatom frustules transported with the food into the canal system by the pseudopods.

spine [acicular spine] – a calcite rod normal to the test surface, thin, round, triangular to triradiate in section, running through a hole in the outer lamella of planktic foraminifera. Arises apparently from the median layer of the chamber wall. At its base it is surrounded by a more or less conical mound, the spine base. Acicular spines are shed during the planktonic life cycle, when descending in the water column prior to reproduction.

spine-base - see spine.

spinose - possessing true, acicular spines (in planktic foraminifera). See also: pseudospinose.

spiral aperture - interiomarginal aperture along a spiral suture. Usually supplementary, not converted into a foramen.

spiral canals - see primary and secondary umbilical spiral canals.

spiral fissure - deep, circular, umbilical space separating ventral chamber tips or folia from an umbilical plug, as in *Ammonia*. Fig. 77.

spiral interlocular space - space formed between adjacent coils along deeply sunken spiral suture. See also: intraseptal interlocular space. Fig. 26.

spiral side - that side of the test in trochospiral forms which contains the proloculus. See also: dorsal.

spiral suture [whorl suture] – the line of adhesion of adjacent whorls in spiral shells.

spiroconvex – a trochspiral shell with a convex spiral side and a flattened to concave umbilical side.

spiroloculine - see milioline coiling.

spirotheca – the free outer wall of fusiform larger foraminifera, in particular of fusulinids, that constitutes the chamber roof and forms a spiral in equatorial section. Deposits on the chamber floor (tectorium, basal layer) of the next whorl are often included in the term. The term's equivalent in discoidal-involute planispiral shells would be "spiral sheet".

stellar chamberlet – an umbilical closed segment of the chamber separated from the main chamber lumen by a folded inner lamella, the stellar septulum. Communicates with its own main chamber lumen through a gap between septulum and the adjacent coil and with the preceding chamberlet through the umbilical part of the preceding foramen. Fig. 48 K & M & Fig. 77 D .

stellate - star-shaped.

stolon – a tubular opening in a chamber wall whose length is greater than its diameter, forming an intercameral foramen that permits communication between consecutive chambers or between cyclical or subsidiary chamberlets of one or two consecutive instars. Fig. 47 A-D.

stolon axis - the axis common to stolons when they are aligned in succeeding septa.

stolon plane - plane defined by stolons that are regularly arranged in layers. Fig. 80.

stolon system – the geometric disposition of stolons in regular patterns.

stratophenetics – the reconstruction of phylogenetic relationships based on morphological (phenetic) similarity on one hand and on the other by the time relationships provided by biostratigraphic ranges, in contrast to cladistics. The most common procedure in the construction of the phyletic lineages of foraminifera. For backup theory see **GINGERICH**, 1990.

streptospiral arrangement - coiled in successively changing planes, like a ball of twine. See also: milioline coiling. Fig. 37.10-11.

striae - thin costae.

striate - having striae.

structure - of foraminiferal shells: a three-dimensional design that defines the morphology of chamber cavities as patterns that are repeated in successive chambers or chamberlet cycles.
Remarks: It is recommended that the term "structure" be employed in a very precise and somewhat restricted way, *i.e.* that it not be used to denote

patterns unrelated to the shaping of chamber lumina, the wall "textures". The term "architecture" should be regarded as having a broader connotation, the combination of textural and structural design with chamber shape and arrangement in the entire test. "Architecture" means the complete set of complex but highly diagnostic characters defining the taxa on the generic level.

style – a massive, imperforate columnar structure between lateral walls supporting expanse chambers that occupy a wide area, as in *Homotrema*.

subembryonic chamberlets – chamberlets that are produced in a mono- or plurilocular third stage in the growth of megalospheric embryos of agglutinated conical foraminifera. They are located below the proloculus in the cone axis and are subdivided by structural elements of uncertain, probably exoskeletal origin. Fig. 41.
Remarks: **J. HOFKER** Jr (1963, p. 211, fig. 14) interpreted the life habit of an orbitolinid as face upward, *i.e.* the cone apex downward, buried in the sediment. Therefore, he called the third growth-stage in *Orbitolina* s.str. "epiembryonic". The confusion up-down is complicated by a supposed error in the legend of fig. 2 in **J. HOFKER** Jr (1966), where deuteroconch and epiembryonic chambers are reversed by comparison with his 1963 paper. Today, all foraminifera with an extensive apertural face covered by numerous apertures live with their apertural face towards the substrate. Undoubtedly, the same is true for conical foraminifera in general. The term epiembryonic is therefore to be avoided. **DOUGLAS** (1960) did not distinguish between sub- and periembryonic chambers, both representing the third growth stage. See also: periembryonic and supraembryonic.

subepidermal partition (-plates, -lamellae) - unspecified, descriptive terms for any kind of structural element subdividing external (lateral) parts of chamber lumen. May be of exoskeletal (beams and rafters) or endoskeletal (septula) nature.

subsidiary chamberlets (secondary chamberlets, auct.) - subdivisions of main chamber lumen by folded inner lamella with the primary organic sheet between folds, or by septula. See also: stellar chamberlets.

succession [ecological succession] – a gradual change over time, in any one area, of the composition of the community through interspecific competition and coexistence, from the arrival of pioneers in an empty habitat to a mature, equilibrated community, termed climax, when equilibrium with long-continued, stable environmental conditions has been achieved. Periodic disturbances in the environment may shorten the length of the succession to early phases of the process (disclimax).

sulcus – a peripheral infold of primary chamber-wall, always imperforate. May or may not have radial passages between the underlying chamber-lumen and the ambient environment or the interlocular space. May or may not be covered by additional marginal structures, such as a marginal cord. Fig. 7 F-G & Fig. 64.
Remarks: **REVETS** (1989, 1993) uses the term sulcus for the adapertural depression between the apertural rim and the attached part of the toothplate. This depression is positioned near or in the axis, not at the periphery of the spiral shell, and should therefore be distinguished from the nummulitid sulcus by a separate term, the "adapertural depression".

supplemental foramen – an orifice produced by a strongly folded toothplate within a protoforamen. May be completely discrete from the protoforamen, as in *Siphogenerinoides*.

supplemental skeleton – the imperforate refolds and flying covers produced by outer lamellae that cover and/or restrict interlocular spaces to form enveloping canal systems, canaliculate spines, marginal crests and marginal cords and the perforate chamberlets that are fed exclusively by canal orifices and that overgrow in more or less regular layers or tires the canalicular structures. The cavities of the supplemental skeleton can not be assigned to particular stages of growth because there is no direct connection with the orderly cameral system of shell cavities. In shells with an extensive supplementary skeleton, the cameral cavity system is reduced to neanic or even nepionic stages. Fig. 65.
Remarks: Introduced by **CARPENTER** (1862) long before lamellar theory was developed, and as now refined here, the term is a welcome complement to the terms exoskeleton and endoskeleton. Both of these terms subdivide the chamber lumen while "supplemental skeleton" structurizes extralocular, "outer" space. It is meant to be used as generic term regrouping all forms that have canaliferous enveloping, marginal and pseudospinose structures

like *Siderolites*, *Pellatispira*, *Calcarina* and their allies along with all types of marginal cords (linked to a single sulcus) as in *Sulcoperculina* and their derivatives, *Ranikothalia* and all nummulitids s.str.

supplementary aperture(s) (secondary aperture(s), pars. auct.) - primarily formed openings either in the apertural face ("apertural pores") or (slit-like) in a sutural position, always in addition to a main cameral aperture. Sutural supplementary apertures are not converted into intercameral foramina because of their position and thus apparently do not serve for passage of functional endoplasm between chambers. The same seems to be true of some multiple supplementary apertures, which - although situated in the septum - may be absent in earlier chambers and/or may be plugged in part at a subsequent instar. See also: accessory apertures.

supplementary chamberlet - a cavity in the supplementary skeleton that is bounded by a bilamellar, perforate wall in the direction of the ambient environment of the shell when it forms. It may be overgrown in later ontogenetic stages by subsequent outer lamellas or by additional elements of the supplementary skeleton. Fig. 63 A & Fig. 65 F.

supplementary spirals – see multiple spirals.

supraembryonic area – in advanced orbitolinids a circular area at the apex of the shell above the megalosphere, formed by a subdivided annular deuteroconch.

supraembryonic chamber – a more or less hemispherical deuteroconch in apical position, embracing from above an often incompletely calcified protoconch bearing exoskeletal elements, as in *Orbitolina* s.str. Fig. 41.
Remarks: This term was introduced by **DOUGLAS** (1960) together with the term "periembryonic" for the third (and partially forth) growth stage, below the proloculus, implying a life position face downward. **SCHROEDER** (1962, 1973) and later **ARNAUD-VANNEAU** (1980) attributed much phylogenetic weight to a distinction between supra- and periembryonic chambers.

surface of attachment – in permanently attached (sessile) shells the surface that is fixed to and casts the substrate. Tiny supplementary sutural apertures in the surface of attachment may indicate that the cell produces some kind of organic glue to stabilize the shell on its substrate.

sutural canals - openings to the exterior of an intraseptal interlocular space whose margins are partly closed by the local adhesion of consecutive chamber walls. See also: fossettes.

sutural supplementary apertures - additions to primary apertures in ventral or dorsal sutural position that are not transformed into an intercameral foramen at the next instar. See also: supplementary apertures.

suture – the line of adhesion of chamber wall(s) to the previously formed test.

symbiont – an organism living together with or within an other organism to the benefit of both.

symbiosis - in foraminifera: algal cells living (as symbionts) within the foraminiferal cytoplasm in a mutualistic relationship with their host. The symbionts actively photosythesize and reproduce asexually in the host cell. They are engaged in recycling nutrients. They live either in vacuoles of the host cytoplasm and are displaced passively by the host's protoplasmic streaming, or are found in the lacunar system of the host cell within which they may move actively using their shortened flagella to regulate the amount of their irradiation by sunlight so as to avoid photoinhibition. During the asexual reproduction of the host, each offspring inherits a small number of symbionts from the mother cell. But after sexual reproduction, the foraminiferal zygote must take up symbionts from its ambient environment. See also: chloroplast husbandry. Fig. 30.

sympatric - inhabiting a common area or largely overlapping areas of distribution. Compare: allopatric.

synonym – a different name for any one taxon. May be invalidated by the priority of the valid name (junior synonym). The names of erroneously identified other valid taxa also appeare in synonymies.

synonymy list – a list in their order of time of their publication of bibliographic references to previous descriptions and/or named illustrations of the taxon considered identical with the taxon being treated and thus a part of the hypodigm.
Remarks:. The synonymy list is an indispensable instrument in taxonomic work justifying the identification of taxa and eventually the creation of new ones. A synonymy list should refer to the type description and in addition reflect the worker's own opinion on the taxon, which may be supplementd where necessary by particular comments. In most cases completeness of synonymy lists is of secondary importance. Copying synonymy lists of previous authors is useless; they may be cited as a block ("with synonymy") if the researcher agrees with the opinion of the previous author in all cases. Disagreements may be listed explicitly under the heading "non". Doubts or approximations of the identity may be expressed by the terms "affinis" (abbreviated aff.) and "confer" (cf.). The former means "near to but not identical", the latter expresses some doubts about the identification, useful in cases where not all diagnostic characters can be identified. Qualified synonymy lists help to enhance and deepen the concept of the taxon under consideration, and expand its documentation. The synonymy list facilitates the establishment of the taxons' range in morphological variation, space and time and permits factual correction of a previous author's work, thus avoiding unnecessary emotions.

syntype – see type.

T

tectorium - in fusulinids: a slightly transparent internal layer of the shell that lines the chamber walls and is covered by the opaque tectum in the external, spiral wall. May be combined with a diaphanotheca.

tectum – in fusulinids: a thin, dense outer (extern) layer of the spirotheca (spiral outer wall), homologous in position to an epiderm but possibly produced by a discrete shell-building process. May bear tiny, pore-like gaps permitting replication of parakeriothecal elements like chomatal pores in a superposed shell layer. See also: marginal prolongation.

template – a sheet of protein substances on which biomineralization initiates. It governs the pattern, shape and size of the biomineralized chamber wall. During chamber growth, the template is put in position by the brush-like pseudopodia prior to the biomineralization of the wall. See also: median layer.

teratological – a pathological alteration of shell morphology, for example a loss of control that maintains axes of coiling or bilateral symmetry consistant. These aberrations are common in gerontic growth stages or after temporary extreme environmental conditions in tidal pools.

terminal - positioned at the distal end of a linear structure or of an elongate chamber.

test – the shell or skeletal components of a foraminifer. The test may be composed of a variety of materials: secreted, agglutinated or in combination.

test-architecture – the spatial arrangement of chambers, their subdivisions and their connections.

test-composition – the mineralogical and chemical composition of test-walls. Compare: texture.

test-structure – any repeated pattern of the elements that subdivide chamber lumina.

test [wall]**-texture** - pattern of arrangement of crystallites, agglutinated grains, organic matter, pores, lamination or layering.

textural ornamentation – the pattern generated by a regular grouping of pores or other textural elements on the surface of a shell. Fig. 75 F-G.

thylacoid – the membrane-bounded, much compressed sac ocurring alone or associated in stacks in the chloroplasts of vegetal cells and in particular in the symbionts of the foraminifera. Traps sunlight as the source of energy for the synthesis of sugars. Fig. 30.

tongue - see toothplate.

tooth (pl. teeth, French: dents) - inward projection(s) of the inner portion of the chamber wall into the aperture. This structural element is a continuation of the basal layer and may be more or less modified but not suppressed when the aperture is transformed into an intercameral foramen. Teeth growing out from the basal layer may be complemented by local thickenings of the inner portion of the free, marginal chamber walls.
Remarks: Teeth may be defined as discrete endoskeletal elements restricted to the apertural area. The relationships between teeth and pillars (in particular those supporting a trematophore) on one hand, to valvular teeth in agglutinated and to toothplates in lamellar-perforate foraminifera on the other is a close one and may be transitional. True teeth must be distinguished from tooth-shaped masks in *Borelis* obstructing the main apertures but resorbed totally in intercameral foramina. See also: milioline tooth.

toothplate (sipho; central pillar, pars auct.) - a contorted plate running from an intercameral foramen to an aperture, and attached to both. It may be shaped to form a single, double or spiral fold (or "tongue") with a free, often serrated distal end and distally protruding into the aperture. A toothplate separates partly or completely the main chamber lumen from an axial space (adapertural depression) in post-embryonic stages. It protrudes with a free edge distally and adaxially into the aperture. Interconnected toothplates in low-trochospiral umbilicate shells may produce a primary spiral canal. A toothplate is never associated with a foliar or stellar chamberlet. The use of the term in low-trochospiral rotaliid forms is under discussion (see **REVETS**, 1993).

topotype – see type.

trabecules [trabeculae] - imperforate shell material extending from an imperforate sutural zone into the perforate lateral chamber-wall and housing oblique, ramified trabecular canals opening between the pores on the surface of the lateral chamber wall (Fig. 81).
Remarks: Trabecules are the result of a deviation of pores from their parallel paths in the lateral chamber wall, to create - in a direction perpendicular to the septum - a V-shaped zone of imperforate wall without inflational deformation of the outer lamellae. In contrast to ordinary elements of ornamentation, they house a trabecular canal with a diameter only slightly larger than that of the pores, and therefore difficult to see in fossil material. The trabecular canals take off from the lateral intraseptal canal in a proximal and/or distal direction and represent therefore an oblique extension of the interlocular space - without folding of the septal flap as in *Planoperculina* - into the stack of outer lamellas. So far, trabeculae have been observed only in some genera of the Nummulitinae, in particular in *Nummulites*, whereas they are absent in *Assilina*.

transverse septulum - see beam.

trematophore – a sieve constituting the face of many porcelaneous larger foraminifera, in miliolids produced by the coalescence of teeth, covering a large preseptal space. May be supported by residual pillars. This construction is in contrast to the multiple apertures produced by the coalescence of peristomal rims, as in *Coscinospira*. Fig. 82.

trichome – leaf hair (of seagrasses for instance). May be casted by the chamberlet walls of foraminiferal epiphytes growing over the leaf surface to strengthen the adhesion of the epiphyte to its substrate. Fig. 42

triconch – the first three chambers in a megalospheric generation separated by plane, uncurved septa. These are shaped by an equilibrated hydrostatic pressure, probably during a single instar. May be enveloped by common secondary lamellas, for example in *Planorbulinella*. Fig. 60 B.
Remarks: **DROOGER** (1993) calls this feature a tritoconch, a term which, however, is preoccupied for the third chamber in megalospheric *Miniacina*. See also: biconch.

triloculine - see milioline coiling.

trimorphism – a morphologic differentiation of the megalospheric generation in A1 and A2. A1 has a comparatively small megalosphere and reaches larger adult shell sizes than A2. The A1 shells are interpreted (**HOFKER**, 1968) as representing diploid schizonts generated by the microspheric agamont. The A2 shells, after the reduction division of the reproductive nuclei in A1, would represent haploid gamonts reproducing sexually. Thus, three different phenotypes would represent a (trimorphic) species. See also: alternation of generations. Fig. 5.

triserial - chamber arrangement in a trochospire with three chambers per coil, hence with about 120° between the median planes of consecutive chambers. See serial disposition of chambers.

tritoconch - the third chamber of the megalospheric embryo of *Miniacina*. It has multiple apertures that feed a more or less concentric chamberlet cycle of the nepionic stage of growth.

trochospiral arrangement - chamber arrangement in whorls or coils where the rate of translation (net rate of movement along the growth axis to the net rate of movement away from the axis) is more than zero. Spiral and umbilical sides are dissimilar. May be involute or evolute on either the spiral or the umbilical side. See also: reversed trochoid.

tube pillars - hollow pillars formed by a folded septal flap, as in *Chapmanina*.

tubercle - see pustule.

tuberculate, papillate, pustulate - covered with tubercles, papillae or pustules. See also: pustule.

tubulin – a globular protein molecule forming the subunits to be polymerized to microtubules.

tubulopore – a pore opening at the end of a conical or tubular projection.

tubulospines, tubulospinate - hollow pseudospines. The cavity is a linear extension of the chamber lumen that ends blindly below the tip of the pseudospines. Caution! Many pseudospines have been erroneously interpreted as hollow (as in *Asterorotalia pulchella*).

tunnel – An intercameral foramen in an interiomarginal-basal position bordered by endoskeletal structures narrowing the communication between the open chamber lumen and the spiral space extending through the successive tunnel foramina. The tunnel is produced by resorption of parts of an apertural face and/or of an apertural mask. May be multiplied to form a single row of basal foramina in fusiform shells. Fig. 31, Fig. 32 A-D & Fig. 66.
Remarks: Introduced originally for fusulinids, where the tunnel is bordered by chomata and may be multiplied - together with the endoskeletal elements, the parachomata - the term has been extended to pfenderinids (**HOTTINGER**, 1978). In this family the tunnel is bordered by being incised in a columellar endoskeleton and may be multiplied as multiple, parallel incisions in such complex genera as *Sanderella*. In addition, the term is extended here to nummulitids where the tunnel is bordered by a pair of umbilical plates in much the same position as the chomata in fusulinids. In nummulitids, no multiplication of tunnels has been observed so far.

type – in taxonomy: the specimen or taxon of next lower rank designated to be always included in the respective taxon and to be excluded from neighbouring taxa, in what ever way that taxon might be defined and/or delimited by subsequent authors. Several kinds of types are distingushed: **holotype**: the single specimen showing all characteristics considered relevant to its identification and segregation at the time of its designation; **syntypes**: several specimens of the type population that together show all characters considered relevant at time of designation; **cotype**: an additional type specimen in support of the holotype; **paratypes**: specimens designated as such in addition to a holotype and considered important for the definition of the species' variability; **topotype**: all specimens of the type population; **lectotype**: a single specimen selected from a series of paratypes, if a holotype has not been designated; **neotype**: a specimen, selected if possible from the original population, to be designated as type if the original holotype has been lost; **plesiotype**: illustrated specimen used for justification of an identified taxon or in support of a redescription of a valid

taxon and deposited in a public collection; **generotype**: type species of a genus.
Remarks: Types play an important role in the revision of fossil taxa. The type specimens of valid species must be deposited in a collection accessible to the public. However, in most cases, the type specimens are not available for further study by any invasive method (coating for Scanning Electron Microscopy, sectionning for structural and geochemical analysis etc.). Therefore revision of a species must be focussed on topotypes. Consequently we recommend, in the proposal of new taxa, that not only the types but also as many topotypes as possible be deposited for further reference. Fossil specimens considered to represent the original (type-) population come from the same field sample or from the same bed at a particular (type-) locality, according to circumstances. The use of syntypes may be justified when the taxon is based exclusively on specimens in cemented rock studied by thin sections. In this case, some diagnostic features may appear only in sections of specific orientation. Otherwise, the use of the various kinds of types is to be limited to the curating of collections in museums. All specimens considered by an author to belong to a taxon are part of the hypodigm, including the specimens of previous authors listed in the synonymy.

U

ultimate chamber – the last chamber formed in an individual.

umbilical [intraumbilical] **aperture** – a primary aperture of a chamber leading into an umbilicus.

umbilical bowl (pseudoumbilicus, pars auct.) - a deep, wide or narrow conical space in axial position formed between inner umbilical chamber walls, wherever the latter are separated from the outer umbilical walls by a distinct edge or shoulder. Compare: umbilicus; pseudoumbilicus. Fig. 12 C.

umbilical canal system - umbilical interlocular space transformed into tubular cavities by various skeletal elements and chamber wall extensions (folia). Commonly modified by local resorption to create a network of communications between the tubular cavities. See also: spiral canal; funnel.

umbilical cavity - the axial complex of interconnected passageways delimited by axial chamber walls, inner umbilical walls, folia, foramenal plates, and cover plates. Includes thus the umbilical canal systems. May be restricted by piles or plugs and communicates with the exterior through foliar apertures or vertical canals.

umbilical depression (umbilicus, pars auct.) - a closed depression in axial position formed by the curvature of the umbilical chamber-walls in the same coil. Compare: umbilicus; pseudoumbilicus).

umbilical flap - rotaliellid extension of the umbilical chamber wall deliminating a narrow umbilicus and covering an umbilical aperture. The anterior margin may be glued to the umbilical wall of chambers in the previous whorl.
Remarks: As the term "umbilical flap" was used earlier as a synonym of "umbilical plate" in rotaliids, its revival for umbilical chamber wall extensions in Rotaliellidae (by **PAVLOWSKI** *et alii*, 1992, fig. 1) leads to confusion and should be abandoned. Instead, umbilical chamber wall extensions in Rotaliellidae should be compared to structures in planktic foraminifera with comparably open, true umbilici and so be designated with corresponding terms.

umbilical plate (foramenal plate; umbilical flap; murus reflectus; toothplate; paries proximus, pars auct.) - a more or less contorted plate-like test element, extending between distal and proximal chamber walls and joined to both, attached to the intercameral foramen and to the main aperture, but not protruding into the latter. Separates the main chamber lumen from a primary umbilical-spiral canal. Between plate and adjacent coil or within the plate itself an opening provides connection between chamber and foliar chamberlet, wherever present.This opening may remain open in all chambers or it may be closed in all but the ultimate chamber by a sealing plate. An umbilical plate may be single or composed of two symmetrical branches in some planispiral genera, thereby producing one or two umbilical-spiral canals between plate and adjacent coil. Fig. 7 F-G, Fig. 54 H & Fig. 63 D.

umbilical plug (-pile, -mass, umbonal plug) – a pile of lamellae forming a solid, more or less free-standing plug in the center of the umbilicus, often separated from foliar tips by a spiral fissure. Fig. 77.

umbilical primary aperture - see umbilical aperture.

umbilical shoulder - see umbilical bowl.

umbilical side - in trochospiral tests the side opposite to the spiral one. See also: ventral.

umbilical teeth - triangular modifications of the lip over umbilical apertures, as in *Globoquadrina*.

umbilicate - possessing a true umbilicus on one or both sides (biumbilicate).

umbilicoconvex - in trochospiral shells: spiral side flattened to concave, umbilical side convex. Compare: spiroconvex.

umbilicus – the axial space in spiral foraminifera communicating directly through apertures with surrounding main chamber lumina or foliar chamberlets. May be open or restricted by an umbilical plug. (Compare umbilical bowl; pseudoumbilicus; umbilical cavity; umbilical depression).

umbo (central pillar, Zentralpfeiler of German authors on nummulitids) – an expanding pile of thickened lamellae in an axial position in involute or orbitoidal foraminifera. An umbo is never associated with an open umbilicus or with spiral umbilical canals. See also: pile; plug. Fig. 77.

unilocular (monolocular, monothalamous) - single- chambered.

uniserial - chambers arranged in a single row. Compare: biserial; triserial. See serial disposition of chambers.

V

vacuolar system (in *Monolepidorbis*) - see lateral chamberlets.

valvular tooth - in agglutinated foraminifera: a flap-like extension from the distal margin of a main aperture, partly restricting it.

veneer - outermost array of more or less blocky or columnar calcite or aragonite crystallites, an integral constituent of the outer lamella in bilamellar foraminifera.

venter – that part of free benthic shells, particularly if flattened, facing the substrate. See also face and surface of attachment.

ventral - the side of a flattened organism turned to its substrate, as opposed to dorsal. Secondarily flattened, almost planispiral or slightly reversed-spiral, involute shells like *Daviesina salsa* (**DAVIES** et **PINFOLD**) or *D. langhami* **SMOUT** reveal their trochospiral phyletic origin by an asymmetric, ventral position of the main cameral foramen and of the umbilical plate. See also: umbilical side; spiral side; remarks to dorsal.

vertical canals (oblique canals, pars auct.) – see funnel.

vestibule (Vorhof in German) – a deuteroconch that embraces a protoconch including its wide-open flexostyle with a hemicylindrical to almost cylindrical frontal wall bearing numerous apertures, as in *Amphisorus* and *Marginopora* (**LEHMANN**, 1961).

vicarious species - closely related, even sister species, occupying identical or very similar niches ("ecological substitutes") in separate regions.

vortex - a helicoidal extension of many consecutive alar prolongations spirally twisted around the coiling axis of a planispiral-lenticular shell. There are transitions to meandrine structures. See also: polar torsion, the equivalent in fusiform shells.

W

whorl [coil] – in a spiral test, a single turn or volution through 360°.

Z

zygote – a diploid cell resulting from fusion of two (haploid) gametes in sexual reproduction. The biomineralized envelope of the zygote is called a microsphere. See also: life cycle.

Acknowledgments

This glossary has a long history going back to international courses on larger foraminifera held during the 1990's as part of the European project COMMETT. At that time, Z. **REISS** (* 1917 - † 1996) suggested the use of the rich illustrations of the monograph on the recent foraminiferal fauna of the Gulf of Aqaba (**HOTTINGER** *et alii*, 1993) as a support of the glossary attached to this work. With the help of V. **SCHEURING** (Basel) this glossary was amplified to include fossil taxa for subsequent COMMETT courses. Most kindly, J. **LIPPS** put the unillustrated glossary on the web in Berkeley. The staff and many participants in the COMMETT courses took an active part in discussing the meaning of terms significant in analyses of the comparative anatomy of the foraminiferan shell, namely A. **ARNAUD** (Grenoble), D. **BASSI** (Ferrara), E. **CAUS** (Barcelona), K. **DROBNE** (Ljubljana), C. **FERRÀNDEZ** (Barcelona), H. **FORKE** (Berlin), M. **LANGER** (Bonn), U. **LEPPIG** (Freiburg i. Br.), J. **PIGNATTI** (Rome), J. **REICH** (Basel), E. **VECCHIO** (Naples) and **E. VILLA OTERO** (Oviedo).
The illustrations of the glossary presented here include a certain number of unpublished plasticine sculptures made by M. **REICHEL** (* 1896 - † 1984) in the nineteen-forties and which since that time have been used for instruction. The TEM graphs, mostly unpublished, are the work of S. **REBER-LEUTENEGGER** (Sissach). The SEM graphs were made in the SEM lab of the University of Basel, at the time directed by R. **GUGGENHEIM** (Basel). Most fossils used to illustrate this glossary were either donated to the Geological Institute by F. **ALLEMANN**, M. **CHATTON**, Z. **REISS** and M. **WANNIER** were collected by the staff of the Geological Institute after 1940 when courses on micropaleontology began at the University. Most of this material is now deposited in the Museum of Natural History in Basel.
With trying efforts N. **SANDER** reviewed and polished the English text while B. **GRANIER** edited the electronic version and contributed many good ideas as to the presentation of the illustrations. D. **BASSI** and an anonymous reviewer gave their opinion on the texts. My sincere thanks to all of them, and also to the many students to whose questions I had no immediate answer.

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Figure 1: Accessory aperture in bulla of *Globigerinita glutinata* (**EGGER**). SEM graph from **HOTTINGER** *et alii*, 1993.
aca: accessory aperture; **bu:** bulla; **ch:** ordinary spiral chamber.

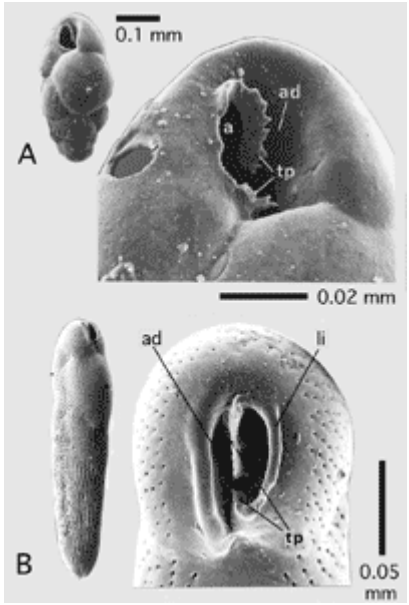


Figure 2: Adapertural depression and toothplate with serrated margin. SEM, from **HOTTINGER** *et alii*, 1993.
A: *Bulimina elongata* d'**ORBIGNY**; **B:** *Loxostomina* cf. *africana* (**SMITTER**).
a: aperture; **ad:** adapertural depression; **li:** lip; **tp:** toothplate with its serrated margin.

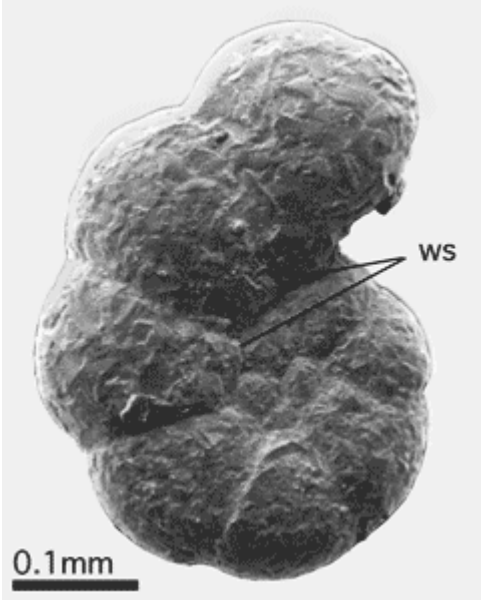


Figure 3: Advolute whorl in agglutinated planispiral shell of *Labrospira jeffreysii* (**WILLIAMSON**). SEM, from **HOTTINGER** *et alii*, 1993.
ws: whorl suture.

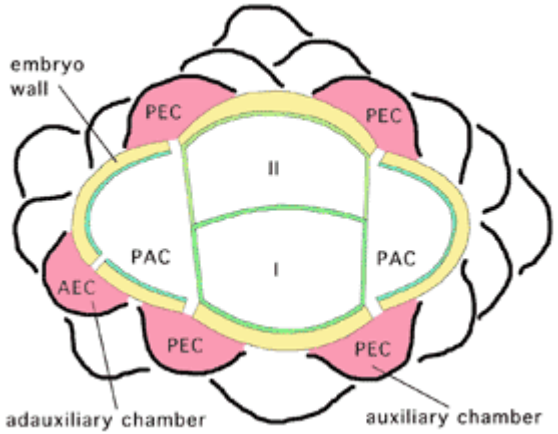


Figure 4: Embryonic and periembryonic chambers in *Orbitoides* spp. according to **VAN HINTE**'s 1966 concept.
I: protoconch; **II:** deuteroconch; **PAC:** principal auxiliary chamber; **PEC:** principal epi-auxiliary chamber; **AEC:** accessory epi-auxiliary chamber. In our view, we prefer to call PAC an auxiliary and AEC an adauxiliary chamber.

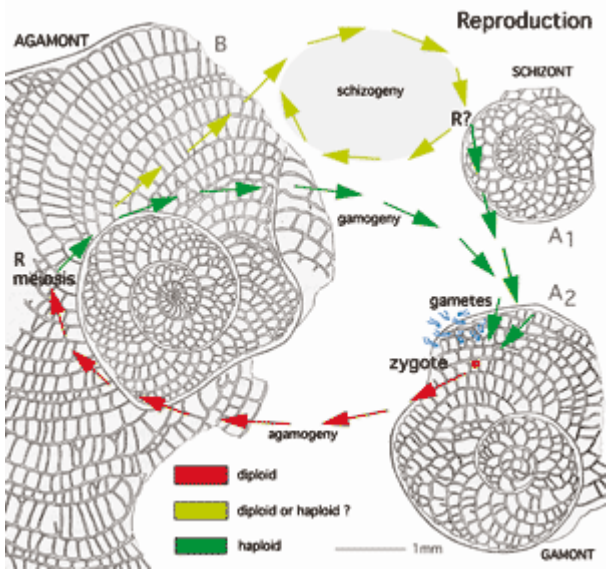


Figure 5: Standard dimorphic or trimorphic reproductive cycle in benthic, medium- to large-sized foraminifera according to **GOLDSTEIN**, 1999. Schizogeny, eventually repeated several times, may be widespread in larger foraminifera from oligotrophic habitats. Planktic foraminifera seem to have no dimorphic life cycle. Life cycles are linked in various ways to seasonal cycles. Example: *Heterostegina depressa* d'**ORBIGNY**, equatorial sections, Gulf of Aqaba, Red Sea (from **HOTTINGER**, 1977).

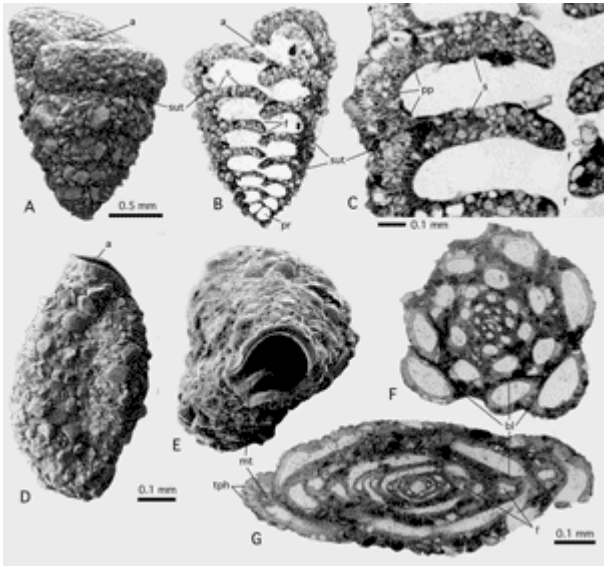


Figure 6: Agglutination in foraminiferan walls; Gulf of Aqaba, Red Sea; Recent.
A-C: *Textularia* sp. C in **HOTTINGER** *et alii*, 1993. **A:** Lateral view showing coarse grains producing a rugged shell surface exept on apertural face. SEM. **B:** axial thin section of the biserial test showing distribution of agglutinated grains within the shell walls. Light microscope, transparent light. **C:** Detail from another specimen showing parapore texture of wall and its relation to the agglutinated grains. Transmitted light. **D-G:** *Agglutinella* sp., an agglutinating, porcelaneous miliolid. **D:** lateral view showing coarse agglutination at the shell's suface. **E:** apertural view showing large aperture with a porcelaneous peristomal rim and a miliolid tooth. SEM. **F-G:** *Schlumbergerina alveoliniformis* (**BRADY**), thin sections in the - and perpendicular to the - apertural axis, showing early growth stages without apparent agglutination and a very thin basal layer coating the rugged surface of adult chambers of the previous whorl. Transmitted light.
a: aperture; **bl:** basal layer; **f:** foramen; **mt:** miliolid tooth; **pp:** parapores; **pr:** proloculus; **s:** septum; **sut:** (chamber) suture; **tph:** trematophore.

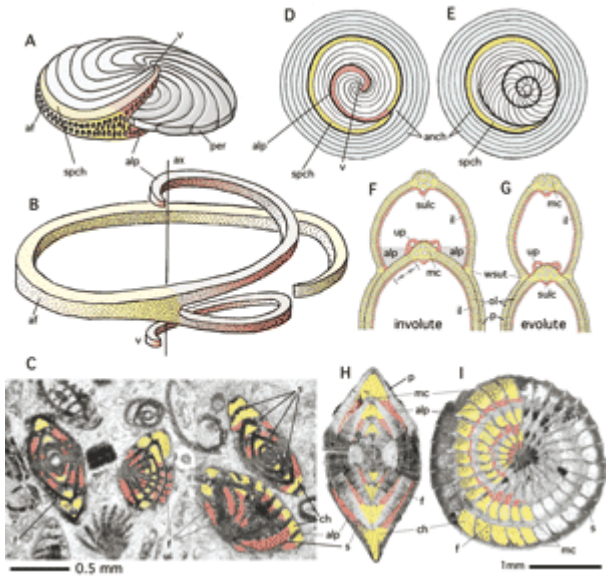


Figure 7: Alar prolongations and involuteness in lamellar foraminifers. **A:** planispiral-involute shell with a long apertural face, as in *Archaias*. Note the apertures in the face of both alar prolongations. **B:** shape of single (penultimate) spiral chamber with long alar prolongations forming a vortex. **C:** Random sections of "*Peneroplis*" *glynnjonesi* **HENSON**, Lower Oligocene, Iran. Transmitted light. Note foramina in the alar septa. **D-E:** Transition from planispiral-involute to annular growth. **D:** external, lateral view of subsequent chambers, showing the ultimate spiral chamber with its alar prolongation and subsequent annular chambers. **E:** all chambers in equatorial section including the tightly coiled nepiont. **F-G:** Involuteness and evoluteness in lamellar foraminifers: an accurate definition is whether or not perforate walls (double arrow) cover the next whorl. Axial section, schematic, not to scale. Note the numerous, outer lamellas (green) enveloping the total exposed surface of the previous shell (compare "lamellation"). The distribution of the inner lamella (red) covering the previous whorl hasno significance in the definition of involuteness. **H-I:** *Nummulites incrassatus* **DE LA HARPE**. Upper Eocene, Northern Italy. **H:** not quite centered axial section. **Red:** lumen of alar prolongation, **yellow:** lumen of equatorial chamber. **I:** oblique section almost perpendicular to shell axis. Note the obliqueness of the intersections of the alar prolongations. **af:** apertural face; **alp:** alar prolongation; **anch:** annular chambers; **ax:** shell axis; **ch:** chamber; **f:** foramen; **il:** inner lamella; **mc:** marginal cord; **ol:** (numerous) outer lamellas; **p:** pore; **per:** periphery (of spiral shell); **s:** septum; **spch:** spiral chamber; **sulc:** sulcus; **v:** vortex; **wsut:** whorl suture.

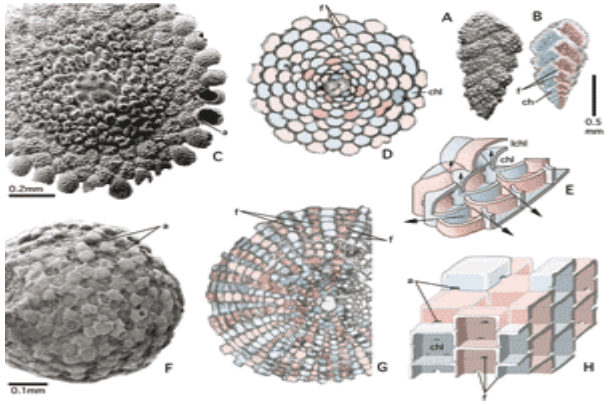


Figure 8: Alternating arrangement of shell compartments in the three dimensions of space. Examples from Gulf of Aqaba, Red Sea; Recent. **A-B:** Alternating chamber arrangement in the linear dimension (= **biserial** arrangement) as in *Textularia foliacea* **HERON-ALLEN** et **EARLAND**, SEM and X-ray graphs of lateral view. **C-D:** Alternating chamberlet arrangement in the planar (second) dimension, as in annular-concentric, discoidal shell of *Planorbulinella elatensis* **THOMAS**, SEM graph of lateral view and equatorial section in transmitted light microscopy, coloured. **E:** Stereograph showing alternating chamberlets of a main chamberlet layer, with main stolon axes (horizontal arrows) and retrovert stolons feeding lateral chamberlet (vertical arrows). Schematic, not to scale. **F-G:** Alternating chamberlet arrangement in the third dimension producing a chessboard pattern, as in the spherical-concentric, globular shell of *Sphaerogypsina globulus* (**REUSS**), SEM graph of external view and centered section in transmitted light micrograph, coloured. **H:** Stereograph showing alternating chamberlets forming **chessboard pattern**. Schematic, not to scale.
Colours: **red** and **blue:** alternating generations of shell compartments; **green:** nepiontic, early stages including proloculus. **a**; aperture; **ch:** chamber lumen; **chl:** chamberlet lumen; **f:** foramen; **lchl:** lateral chamberlet lumen.

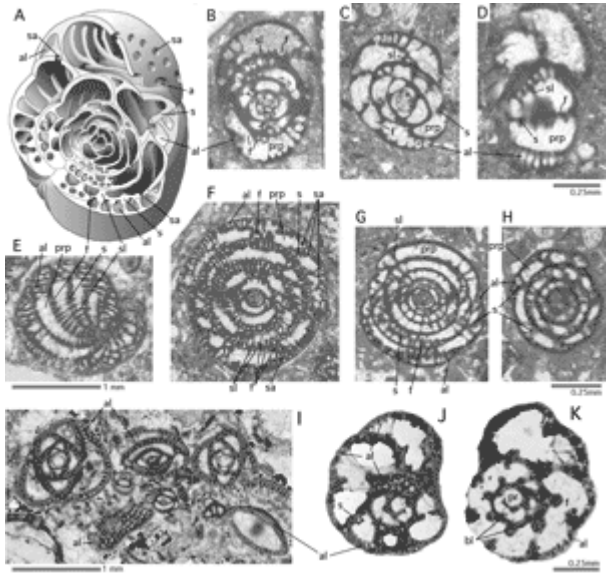


Figure 9: Alveoles.
A-D: model (schematic, not to scale) of the genus *Malatyna* **SIREL**, subaxial, subequatorial and tangential sections. Igualada, North-Eastern Spain. Uppermost Middle Eocene. **E-F:** *Globoreticulina iranica* **RAHAGHI**, tangential and axial sections. Shiraz, Iran. Middle-Upper Eocene. **G-H:** *Bullalveolina bulloides* **REICHEL**, axial and subequatorial sections. Peribetics, South-Eastern Spain. Lower Oligocene. **I:** *Austrotrillina striata* **ADAMS**, sections perpendicular to apertural axis and tangential sections. Kirkuk, Iraq. Oligocene. **J-K:** *Everticyclammina virguliana* (**KOECHLIN**), equatorial sections. Mechra Klila, North-Eastern Morocco, Uppermost Jurassic. All sections transmitted light micrographs.
a: (main) aperture; **al:** alveole; **bl:** basal layer; **f:** (main) foramen; **pr:** proloculus; **prp:** preseptal passage (in these cases extending over most of the chamber lumen); **s:** septum; **sa:** supplementary aperture; **sl:** septular ridges (incomplete septula).

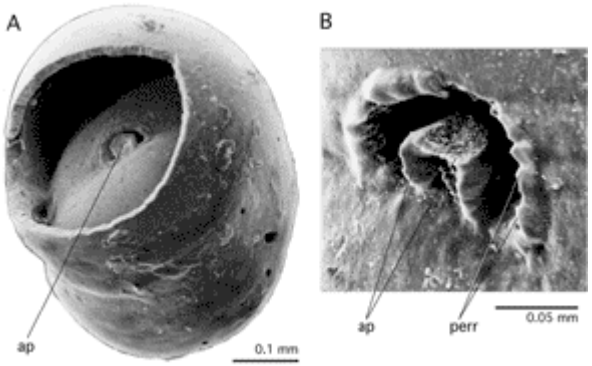


Figure 10: Apertural plate: Apertural feature in *Sphaeroidina bulloides* d'**ORBIGNY**.
A: dissected specimen showing penultimate foramen, **B:** detail of aperture. SEM graphs. Recent, Gulf of Aqaba.
ap: apertural plate; **perr:** peristomal, pustulose rim.

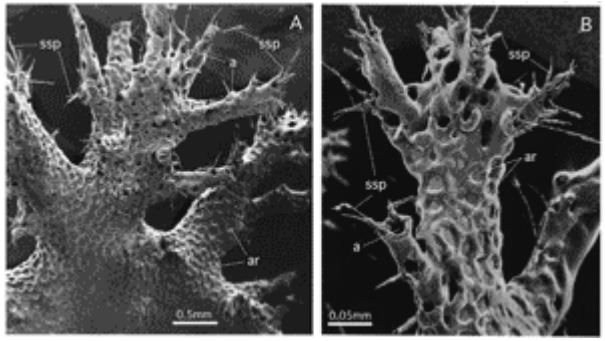


Figure 11: Arborescent shell ornamented by areoli: *Homotrema rubra* (**LAMARCK**), arborescent habit, SEM graphs, Recent, Gulf of Aqaba.
A: overview of arborescent shell, **B:** detail of a single branch, Note the sponge spicules (**ssp**) glued into the tubular peristomal extension of the aperture to serve as fishing rods that support filiform pseudopodia extending into turbulent water for the capture of food.
a: aperture; **ar:** areoli.

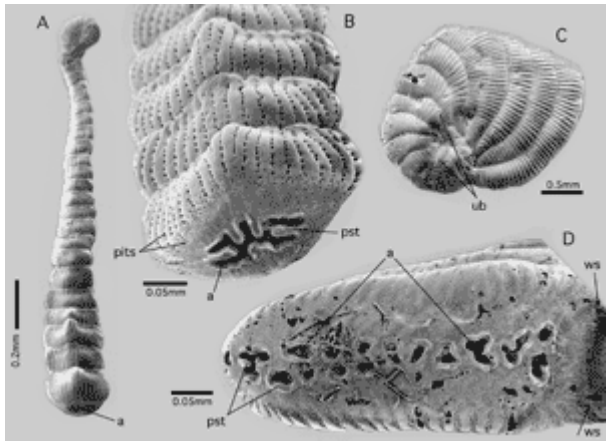


Figure 12: Single and multiple areal apertures.
A-B: *Monalysium acicularis* (**BATCH**); **C-D:** *Peneroplis planatus* (**FICHTEL** et **MOLL**), both from the Gulf of Aqaba, Red Sea, Recent. SEM graphs. Note the presence of pits in the porcelaneous wall and the umbilical bowl characterizing *P. planatus*.
a: areal aperture(s); **pst:** peristomal rims; **ub:** (delimitation of) umbilical bowl; **ws:** whorl suture. Note the absence of interiomarginal apertures.

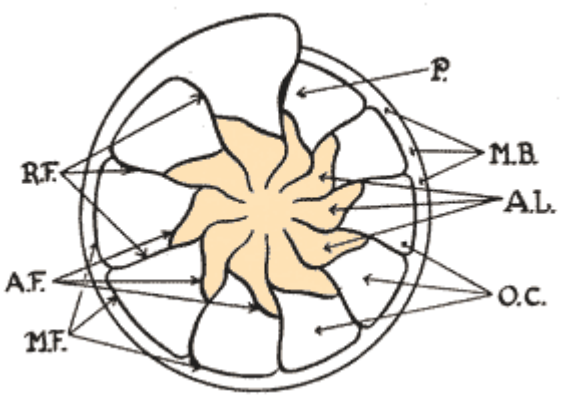


Figure 13: Astral lobes: Original figure from **DAVIES**, 1932, p. 414.
AF: astral furrow (= foliar suture); **AL** (coloured): astral lobes (= folia): **MB:** marginal band (= keel); **MF:** marginal furrow (= septal suture); **OC:** outer chambers; **P:** pylome (= aperture); **RF:** radial furrows (= chamber sutures).

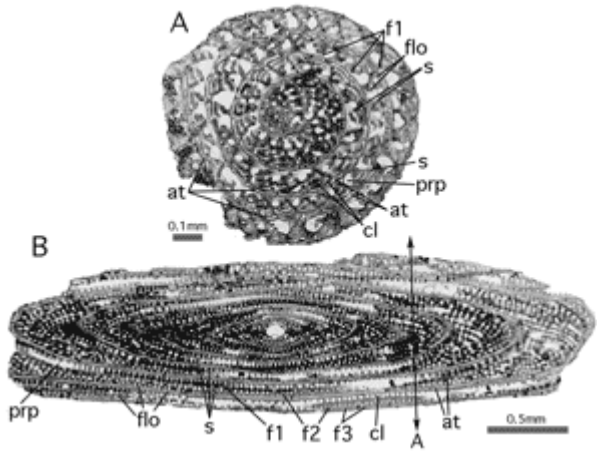


Figure 14: Attics and floors in *Alveolinella borneensis* **TAN SIN HOK**, Molukkas, Miocene. Transmitted light micrographs.
A: Transverse section. Position in respect to B: double arrow A. **B:** axial section.
at: attics; **cl:** chamberlet; **f1:** foramen (basal row): **f2:** foramen (second row); **f3:** supplementary foramina corresponding to the attics; **flo:** floors; **s:** septum.

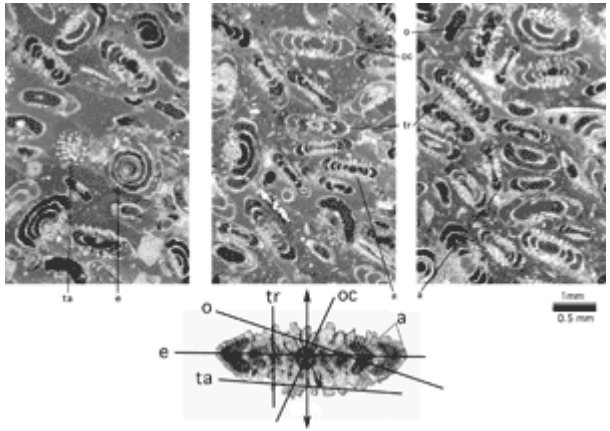


Figure 15: Sections of *Involutina liassica* (**JONES**). Middle Lias, from Arzo, Ticino, Southern Switzerland. Transparent light micrographs. *Involutina* exhibits a lamellar-perforate, planispiral-evolute, dimorphic shell with a spherical megalosphere followed by a tubular chamber cavity without septa. Lateral walls ornamented by protuberant piles between coarse pores. Double arrow: shell axis.
a: axial section; **e:** equatorial section; **o:** oblique section; **oc:** oblique-centered section; **ta:** tangential section; **tr:** transverse section.

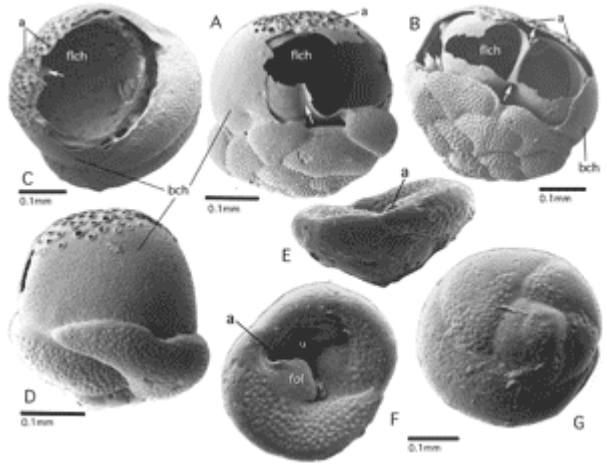


Figure 16: Balloon and float chambers in pseudoplanktic forms. All specimens from the Gulf of Aqaba, Red Sea, Recent. SEM graphs.
A-B: *Cymbaloporetta* sp. Lateral views of dissected specimens. Note tubular infolds of the float chamber canalizing the hatching from the umbilical cavity to the preseptal space under the apertures of the balloon chamber (**arrows**). **C-D:** *Tetromphalus bulloides* (d'**ORBIGNY**). Lateral views of dissected and intact specimens in their pseudoplanktic stage. **E-G:** *T. bulloides* in its benthic stage, showing open umbilicus, lateral, umbilical (ventral) and spiral (dorsal) views.
a: aperture; **bch:** balloon chamber; **flch:** float

chamber; **fol:** folium; **u:** umbilicus.

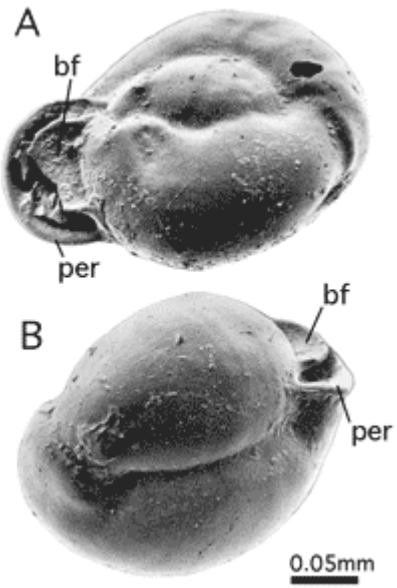


Figure 17: Basal flap in *Miliolinella* sp. from the Gulf of Aqaba. Recent. SEM graphs.
bf: basal flap; **per:** peristomal lip, everted.

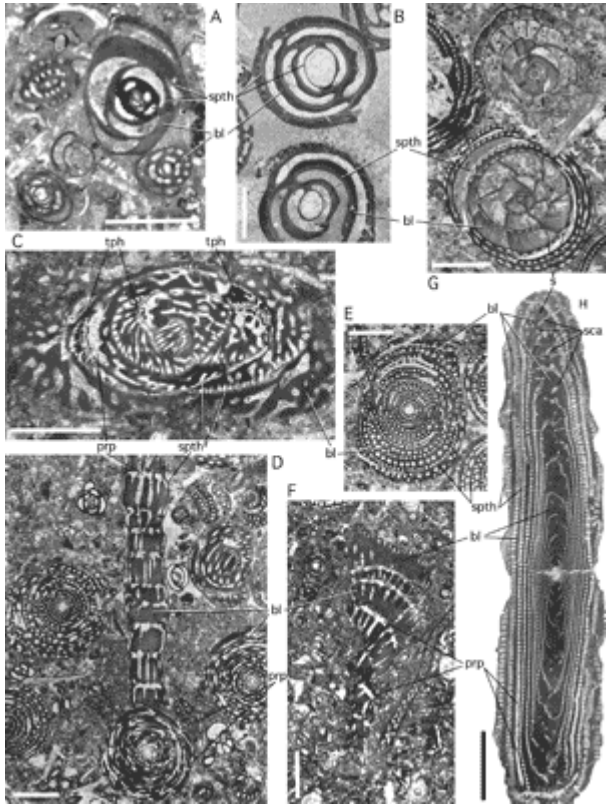


Figure 18: Basal layer and flosculinisation.
A: Unidentified, large miliolid, *Fabularia roselli* **CAUS** and *Dendritina* sp. Randomly oblique sections. Uppermost Middle Eocene, Spanish Pyrenees. **B:** *Idalina antiqua* **MUNIER-CHALMAS** et **SCHLUMBERGER**. More or less centered, subaxial sections. Santonian, Spanish Pyrenees. Note the proloculus wall illustrating the reduced thickness of the outermost layer of the primary chamber wall. The difference in the opacities of the basal layer and the primary outer chamber wall demonstrates how dissimilarly the discrete submicroscopic, porcelaneous wall textures react to diagenesis. **C:** *Fabularia verseyi* **COLE**, oblique section, from Jamaica, Middle Eocene, showing irregular tubiform, anastomosing passages in the basal layer. **D-F:** random sections of *Pseudochubbina globularis* (**SMOUT**), subspherical, and *P. kassabi* **DE CASTRO**, flaring, showing parallel, rarely anastomosing tubiform passages in the basal layer, and an outer layer of more regular parallel chamberlets similar to attics, as also in *Fabularia*. Note the thin spirotheca extending into a lateral cover of the flaring portion of the test. Campanian, Iran. **G:** *Alveolina daniensis* **DROBNE**, oblique sections near the equatorial plane. Compaction of the sediment has mechanically separated outer from inner whorls, revealing the thin spirotheca. Note lines of accretion parallel to the septum in the basal layer of flosculinized whorls. Lowermost Eocene, Slovenia. **H:** *Alveolina tenuis* **HOTTINGER**, axial section, showing columella produced by polar thickening of the basal layer. Note tubular passages in the columella, continuous in subsequent chambers, without interruption by preseptal spaces. Middle Eocene, Aquitaine, Southwestern France.

Abbreviations: **bl:** basal layer; **prp:** preseptal space or passage; **s:** septum; **spth;** spirotheka (outer wall of sucessive spiral chambers); **tph:** trematophore. Scale bars: 1mm.

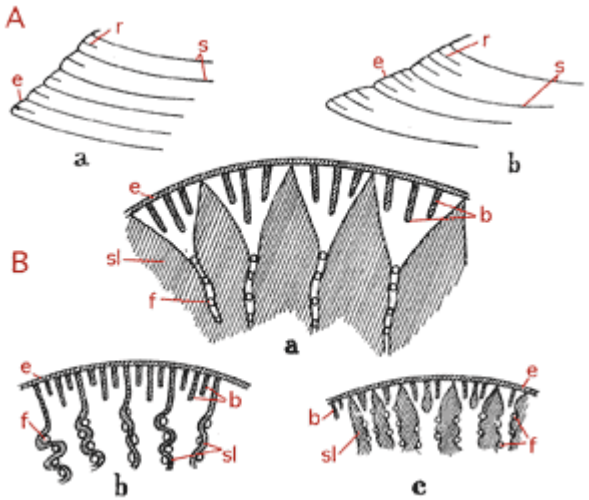


Figure 19: HENSON's "subepidermal partitions" (1948, text-figs. 6-7). **A:** axial sections of uniserial cones (as in Orbitolinidae) with (a) "primary subepidermal plates" and (b) with "primary and secondary subepidermal plates". **B:** basal sections of radial zone showing in addition to "radial plates" (a) "thick, straight radial partitions, (b) "thin radial partitions in zigzag" and (c) "subepidermal plates thickening inward". Compare Fig. 71.
Current interpretation given in red: **b:** beam (perpendicular to septum); **e:** epiderm; **f:** foramina (in Orbitolinines forming a crosswise-oblique pattern); **r:** rafter (parallel to septum); **s:** septum; **sl:** septulum (may fuse with beam).

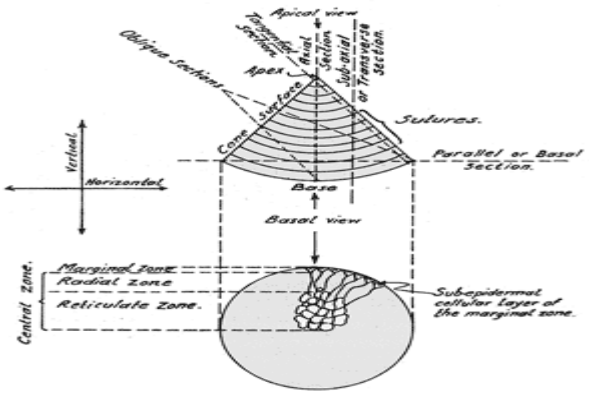


Figure 20: **HENSON**'s "zonation" of discoidal chambers in uniserial-conical shells, namely the marginal, radial and reticulate zones. Compare Fig. 71. From **HENSON**, 1948.

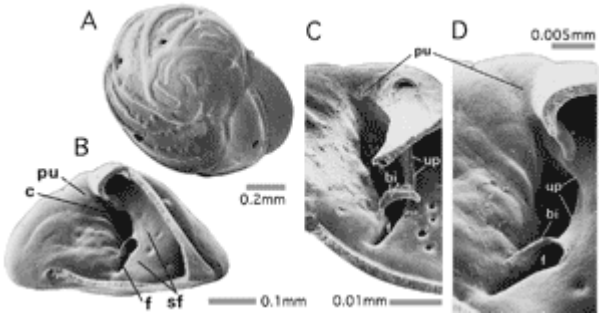


Figure 21: Bipartitor and pseudoumbilicus in *Eponides repandus* (**FICHTEL** et **MOLL**) from the Gulf of Aqaba, Red Sea, Recent. SEM graphs.
A: dorsal (spiral) view, **B:** lateral view of dissected specimen. **C:** oblique umbilical view of dissected specimen. **D:** detail of rotated oblique umbilical view.
bi: bipartitor; **c:** spiral umbilical canal; **f:** foramen; **pu:** pseudoumbilicus; **sf:** septal face: note supplementary apertures closed by septal flap covering the septal face; **up:** umbilical plate.

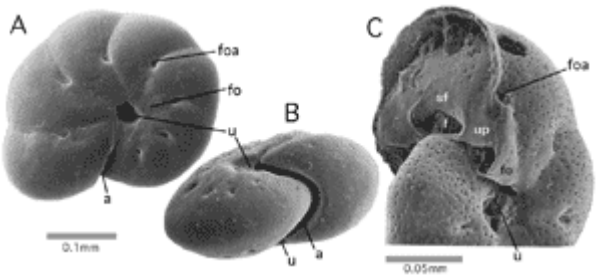


Figure 22: Biumbilicate shell in *Astrononion* sp. from the Gulf of Aqaba, Red Sea, Recent. SEM graphs.
A: lateral view; **B:** apertural view; **C:** oblique view of dissected specimen showing structural details.
a: aperture; **f:** foramen; **fo:** folium; **foa:** foliar aperture; **sf:** septal face, covered by septal flap; **up:** umbilical plate; **u:** umbilicus, on both sides of the test.

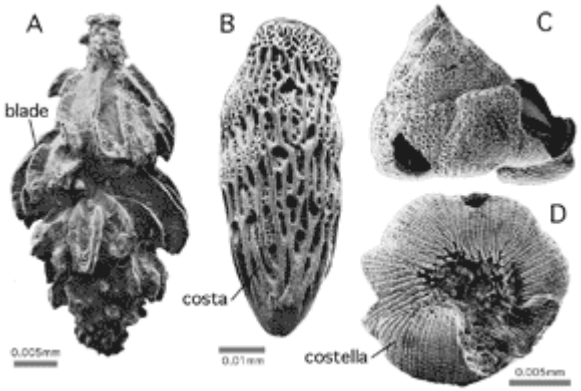


Figure 23: Blades, costae and costellae, linear-elongate ornaments of lamellar-perforate shells.
A: *Neouvigerina porrecta* (**BRADY**), lateral view; **B:** *Loxostoma amygdalaeformis* (**BRADY**), lateral view; **C-D:** *Glabratellina* sp., lateral and umbilical views. SEM graphs. Gulf of Aqaba. Recent.

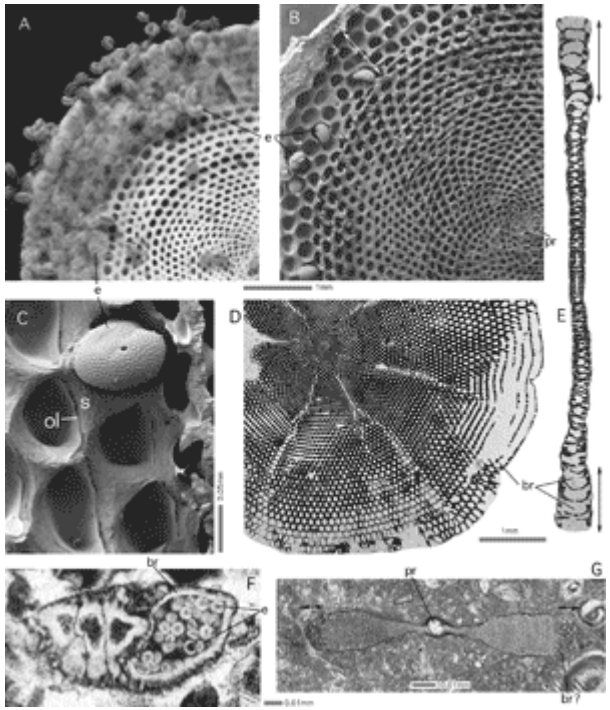


Figure 24: Brood chambers in agamonts of (**A-C**) *Sorites orbiculus* (**FORSKAL**) and (**D-E**) *Amphisorus hemprichii* **EHRENBERG**, all from the Gulf of Aqaba. Recent.
A: fresh hatching on empty mother shell under water. **B:** agamont shell, dried

and split open in the equatorial plane. Some embryos remain in situ in the brood chambers. Note size of microspheric proloculus. SEM graph. **C:** detail of B showing embryo (consisting of proloculus and flexostyle) and surface of resorption including the organic lining. **D:** equatorial and **E:** axial sections showing an abrupt increase in the irregularity and volume of the chamberlet cavity in the last few chamberlet cycles (**double arrows**) marking the brood chambers. **F:** *Neorotalia* sp., thin section parallel to and near the axis of coiling, the last chamber filled with hatchlings. Transparent light micrograph. Spanish Pyrenees, Lower Eocene. **G:** *Orbitolites* sp. Oblique-centered thin section, transmitted light micrograph. Note the discrepancy between embryo size and brood chamberlet volumes: we are in presence of either a gamont producing small gametes or zygotes, or of a schizont keeping the offspring in regular broodchambers prior to the first, prolocular shell formation. Lowermost Eocene, Farafrah Oasis, Egypt.
br: brood chamber; **e:** embryo; **ol:** organic lining; **pr:** proloculus; **s:** septum.

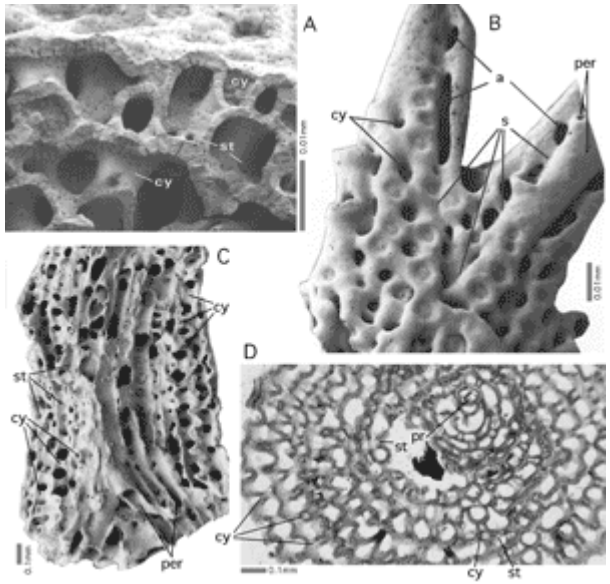


Figure 25: Calyces in arborescent *Miniacina miniacea* (**PALLAS**) from the Gulf of Aqaba. Recent.
A: Fragment broken perpendicularly with respect to the axis of the branch, showing an exterior view of the broken funnel walls of the calyces. SEM graph. **B:** External view of a branch tip showing calyces and apertures at the limiting suture of the expanse chamber that covers previously formed tubular peristomes. SEM graph. **C:** Fragment broken in the axial plane of branch. SEM graph. **D:** Thin section perpendicular to the stem axis of the shell. Transmitted light micrograph. Calyces cut obliquely produced characteristic undulating intersections.
a: apertures in marginal position, to be transformed into stolons when overgrown by a subseqent expanse chamber; **cy:** calyx; **per:** tubular peristome either terminal or overgrown by subsequent expanse chambers; **pr:** proloculus; **s:** marginal suture of expanse chamber; **st:** stolon.

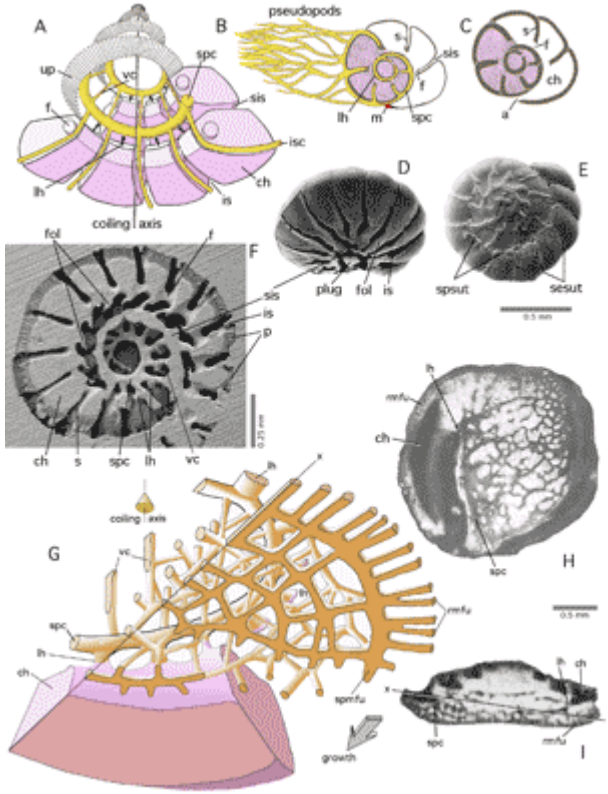


Figure 26: Canal systems.
A: basic geometry of canals in simple rotaliid shells. Schematic, not to scale. **Red:** chamber plasm; **yellow:** canal plasm. **B-C:** during stages of retraction of the chamber plasm into the interior of the shell, the canal system provides motility to the organism by extruding the pseudopods through backdoors, so-called loop-holes. **D-F:** *Challengerella bradyi* **BILLMAN** *et alii*. Gulf of Aqaba, Red Sea; Recent. SEM graphs. **D:** oblique-ventral view of umbilical face; **E:** dorsal (spiral) view; **F:** Epoxy resin cast of shell cavities showing canal system. **G-H:** *Hottingerella chouberti* (**HOTTINGER**), Northeastern Morocco, Lower Cretaceous. Schema after **HOTTINGER**, 1976, not to scale, and transmitted light micrographs. Note that the basic geometry with loop-holes in a shell lacking septal subdivision is similar to a rotaliid with chambers.
a: aperture: **ch:** chamber; **f:** foramen; **fol:** folium; **is:** interlocular, intraseptal space; **isc:** ingtraseptal canal; **lh:** loop-hole; **m:** mask; **p:** pores; **rmfu:** radial marginal furrows (open to the ambient environment for their full length prior to being covered by the next whorl); **s:** septum; **sesut:** septal sutures; **sis:** spiral interlocular space; **spc:** spiral canal; **spmfu:** spiral marginal furrow; **spsut:** spiral suture (between successive whorls); **up:** umbilical plate (general geometric position); **vc:** vertical canals (at umbilical chamber suture); **x:** approximate position of section.

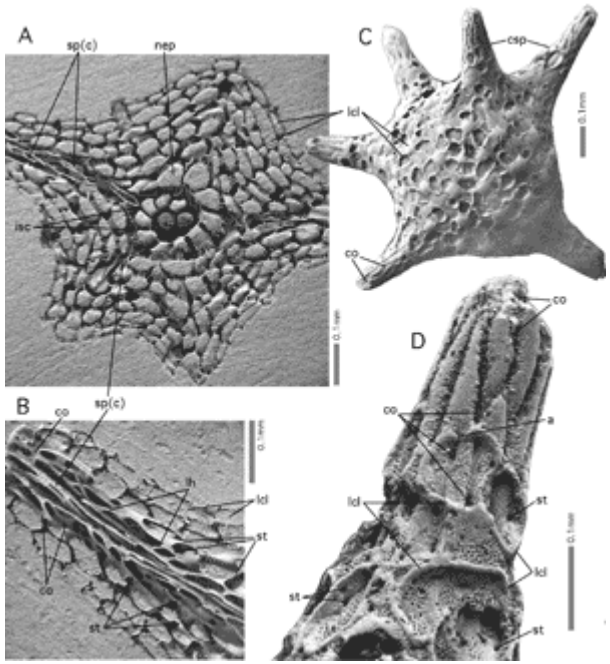


Figure 27: Canaliferous spines in *Baculogypsina sphaerulata* (**PARKER** et **JONES**), Keij Island, Indonesia. Recent. SEM graphs. **A-B:** Epoxy resin casts of shell cavities, the mineralized shell having been dissolved, showing that spine canals originate as extensions of an intraseptal interlocular space, that is then transformed into canals. They feed in their turn the supplemental chamberlets overgrowing the base of the spine. **C-D:** Shell showing chessboard pattern of supplemental chamberlets, overgrowing the base of the canalled spine and fed in part by the overgrown canal orifices. **a:** aperture (of lateral chamberlet); **co:** canal orifice; **csp:** canalicular spine; **lcl:** lateral chamberlet; **lh:** loop-hole; **nep:** (spiral) nepiont; **sp(c):** spine canals; **st:** stolon.

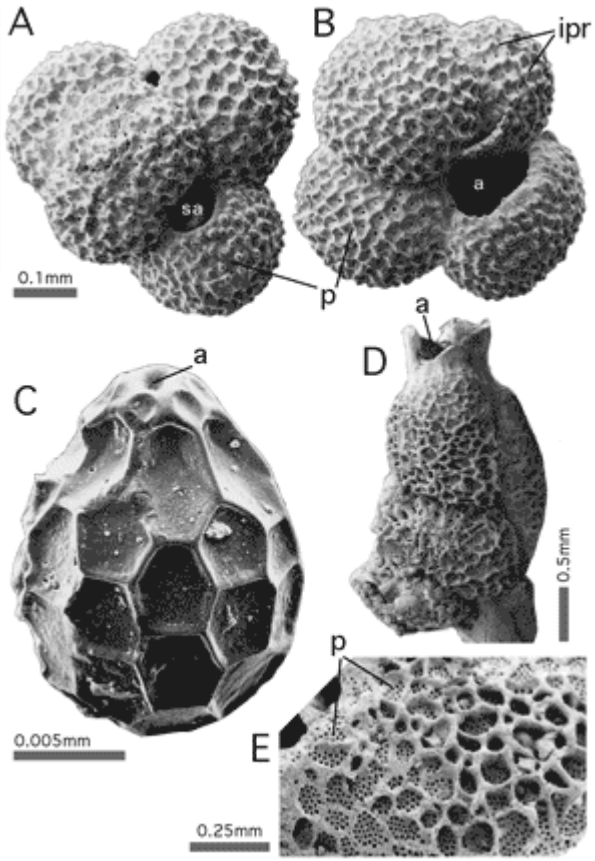


Figure 28: Cancellate ornament in planktic and benthic forms.
A-B: *Globoturborotalites tenella* (**PARKER**), dorsal view showing supplementary apertures. The cancellate pattern is produced by interpore ridges. **C:** *Favulina hexagona* (**WILLIAMSON**) showing a very regular pattern. **D-E:** *Carpenteria utricularis* (**CARTER**) showing a more irregular pattern of ridges delimiting areoli with many pores. All from the Gulf of Aqaba. Recent.
a: aperture; **ipr:** interpore ridge; **p:** pores; **sa:** supplementary aperture.

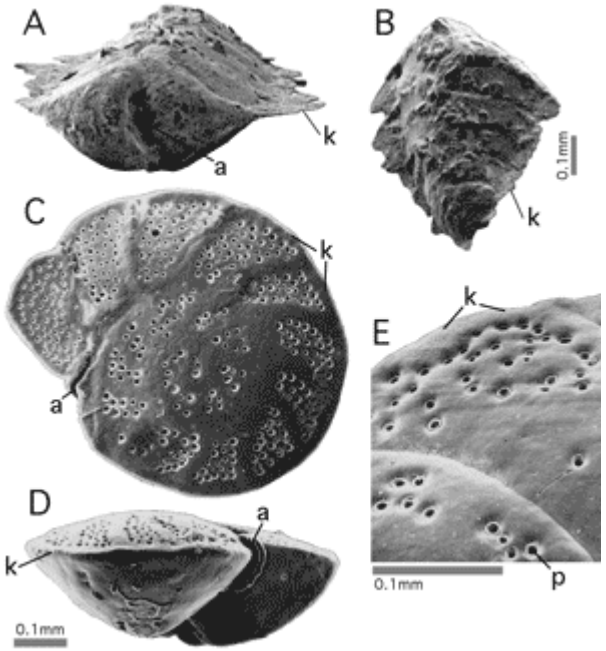
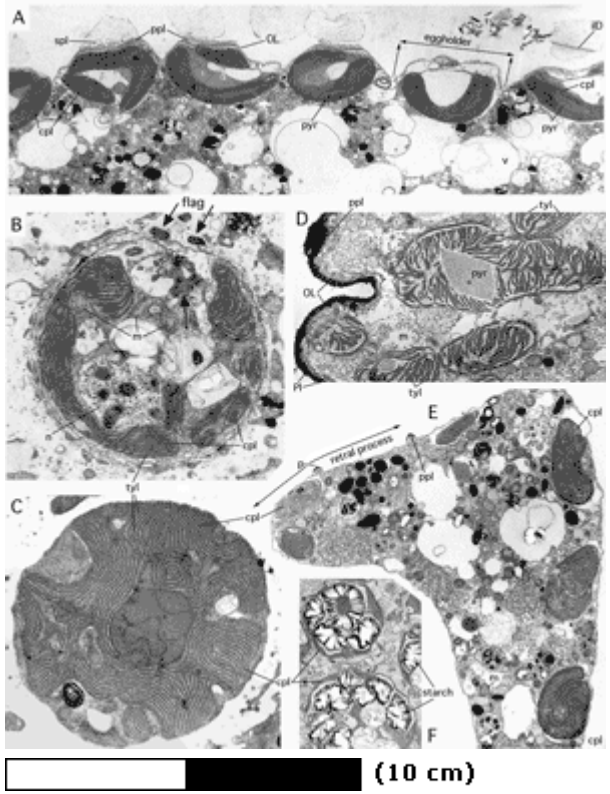


Figure 29: Carina (keel).
A-B: *Spiroplectammina* cf. *taiwanica* (**CHANG**), apertural view and side view. **C-E:** *Paracibicides edomica* **PERELIS** et **REISS**, dorsal (spiral) view, peripheral view and detail of perforation pattern along the peripheral carina on the dorsal surface. Note the interiomarginal, extraumbilical - equatorial position of aperture. All specimens from the Gulf of Aqaba. Recent. SEM graphs.
a: aperture; **k:** carina (keel); **p:** pore.



The magnification of each figure is in proportion to the length of the 10 cm scale bar above.

Figure 30: Chloroplasts of foraminiferal symbionts. Gulf of Aqaba. TEM graphs courtesy **S. REBER-LEUTENEGGER**.
A: Bacillarian (diatom) symbionts below lateral chamber wall, housed in eggholders, below pore mouths, of *Amphistegina lobifera* **LARSEN**. x 5,000. **B:** dinophycean (dinoflagellate) symbiont of *Amphisorus hemprichii* **EHRENBERG**. Note sections of short flagellae (**arrows**) permitting active movement of the symbiont within the lacunar system of the host, to regulate its access to light. The nucleus with its (polyploid) chromosomes visible during the interphase unusual among eucaryotes but characteristic for dinophyceans. x 10,000. **C:** rhodophycean (red algal) symbiont of *Peneroplis planatus* (**FICHTEL** et **MOLL**). x 12,000. **D:** Bacillarian symbiont of *Assilina ammonoides* (**GRONOVIUS**), ultrathin section oblique-tangential to the lateral surface of achamber. Note the loose stacking of the thylacoids in the chloroplast, a characteristic of symbionts of *Assilina*. x 8,000. **E:** *Elphidium craticulatum* (**FICHTEL** et **MOLL**), ultrathin section through a protoplast of a chamber including one of its retral processes (double arrow), showing free chloroplasts in the host chamberplasm, a characteristic of symbiont husbandry. x 4,000. **F:** Rhodophycean symbionts of *Peneroplis planatus* (**FICHTEL** et **MOLL**) from Elba in the Mediterranean. Note starch grains covering the pyrenoid and filling most of the symbiont's mass. The starch grains may also appear as free grains in the host chamber plasm and represent seasonal food storage for the host. x 4,000.

bD: basal pore disc; **cpl:** chloroplast; **flag:** flagellum with its base; **ilD:** interlamellar disc of pore; **m:** mitochondrium; **n:** nucleus; **OL:** organic lining; **p:** pore; **Pl:** plasmalemma; **ppl:** pore plug; **pyr:** pyrenoid; **spl:** (mineralized) sieve plate; **tyl:** thylacoid; **v:** vacuoles.

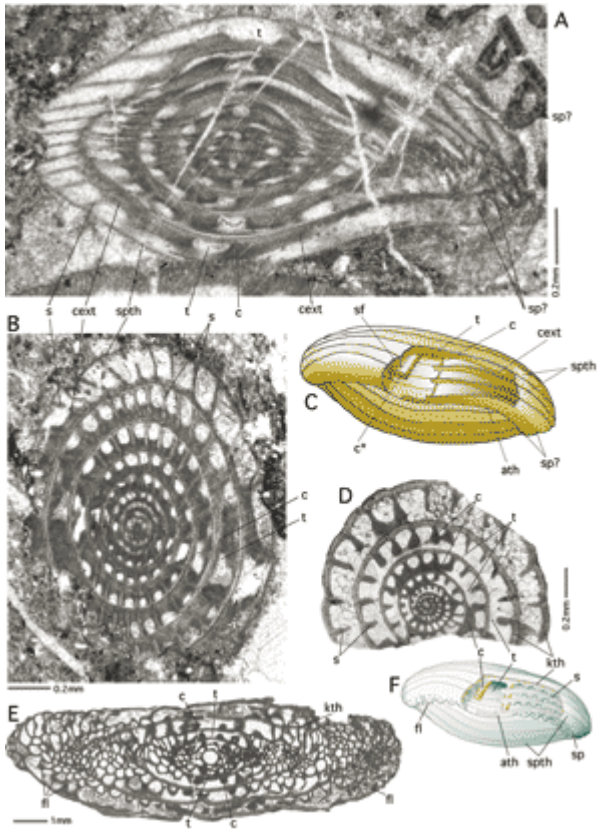


Figure 31: Chomata.
A-C: *Eowedekindellina* sp. Permian, Iran, **ALLEMANN** collection, oblique, subaxial and subequatorial sections, transmitted light micrographs, and model. Note poleward extension of chomata forming a basal layer. **D-F:** ordinary chomata in *Triticites* sp., equatorial and axial sections, transmitted light micrographs and model. Lower Permian, Spitzbergen. Note in D the sector-wise appearance and disappearance of the chomata due to the slight obliquity of the section.
ath: antetheca; **c:** choma; **c*:** cutoff choma stressing the uncertainty about the connection between the choma and the antetheca; **fl:** fluted septa; **kth:** keriotheca; **s:** septum; **sp:** septal pores; **spth:** spirotheca; **t:** tunnel.

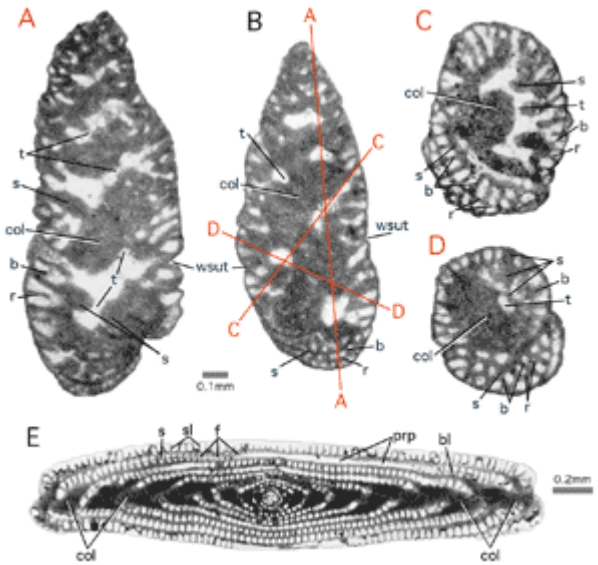


Figure 32: Columellas. Transmitted light micrographs.
A-D: *Kurnubia palastiniensis* **HENSON**. Upper Jurassic, Northeastern Morocco. **A:** transverse section near and almost parallel to the axis of coiling; **B:** axial section; **C-D:** oblique sections. Position of sections relative to the axial section marked by red lines. **E:** *Borelis schlumbergeri* (**REICHEL**), axial section. Gulf of Aqaba. Recent. Note double columella in planispiral-fusiform shells.
b: beam; **bl:** basal layer; **col:** columella; **f:** foramina; **prp:** preseptal passage; **r:** rafter; **s:** septum; **sl:** septulum; **t:** tunnel; **wsut:** whorl suture.

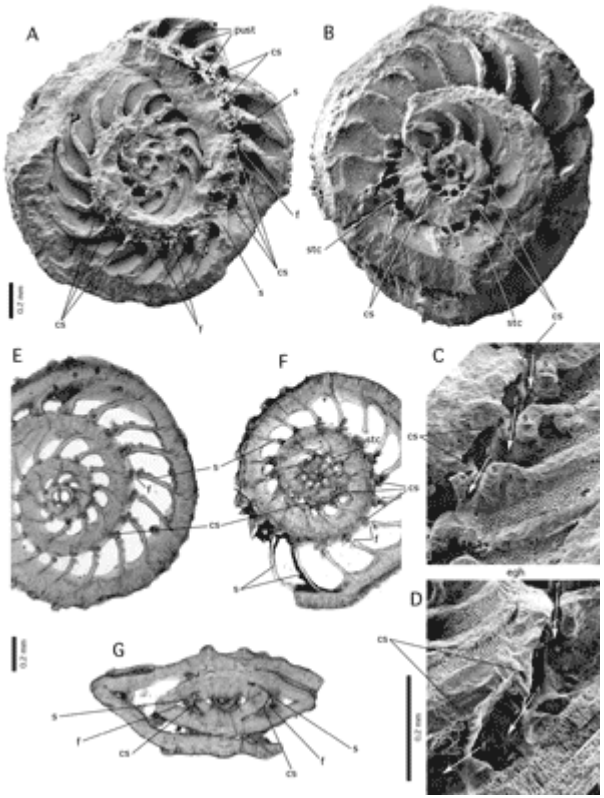


Figure 33: Countersepta.
A-D: *Amphistegina tuberculata* **BERMUDEZ**, Dominican Republic, Upper Miocene, SEM stereographs showing the split halves of a megalospheric shell. **A:** dorsal side in ventral view, **B:** ventral side in dorsal view, with details in **C** and **D**. **E-G:** *Amphistegina lopeztrigoi* **PALMER**, thin slides in transmitted light micrographs, Eocene, Florida. Generic and specific name are unclear and need revision. **E:** centered section perpendicular to the coiling axis; **F:** section perpendicular to the coiling axis located below the megalosphere; **G:** poorly centered axial section.
cs: counterseptum; **egh:** eggholder; **f:** main foramen; **pust:** pustules covering successive faces; **s:** septum of main chambers; **stc:** stellar chamberlets.

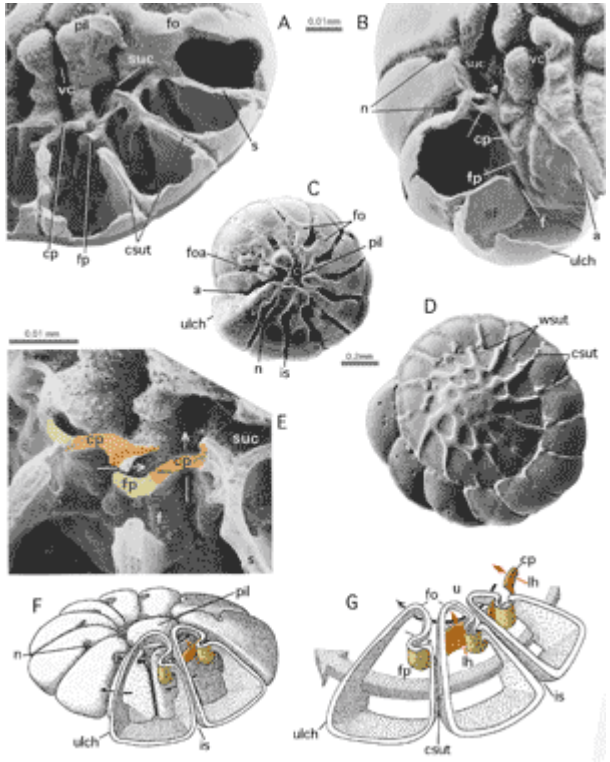


Figure 34: Cover plate and foramenal plate in *Challengerella bradyi* **BILLMAN** *et alii* from the Gulf of Aqaba. Recent. SEM graphs. **A-B:** dissected specimens in oblique ventral view. **C:** young specimen, ventral view. Note incipient umbilical pile against which the foliar walls are beginning to fuse, covering the spiral interlocular space. **D:** dorsal (spiral) view of adult megalospheric specimen. **E:** Detail showing foraminal and cover-plates. Colours corresponding to those used in the models. White arrow: loop-hole. **F:** general model showing position of plates and communications. Note position of loop-hole (red arrow). **G:** Detail of umbilical structures in last three chambers. Note the separation of streaming chamber plasm through successive foramina (blue arrow) and circulation in the umbilical interlocular space (black arrow) by the umbilical structures. Models schematic, not to scale, after **HOTTINGER**, 2000.
a: aperture; **cp:** coverplate; **csut:** chamber (septal) suture; **f:** foramen; **fo:** folium; **foa:** foliar aperture; **fp:** foramenal plate; **isp:** interlocular (intrasepal) space; **lh:** loop-hole; **n:** notch; **pil:** umbilical plug; **s:** septum; **sf:** septal flap; **suc:** spiral umbilical interlocular space, transformed into spiral canal when covered by foliar extensions; **u:** umbilicus; **ulch:** ultimate chamber; **vc:** funnel (vertical canal); **wsut:** whorl (spiral) suture.

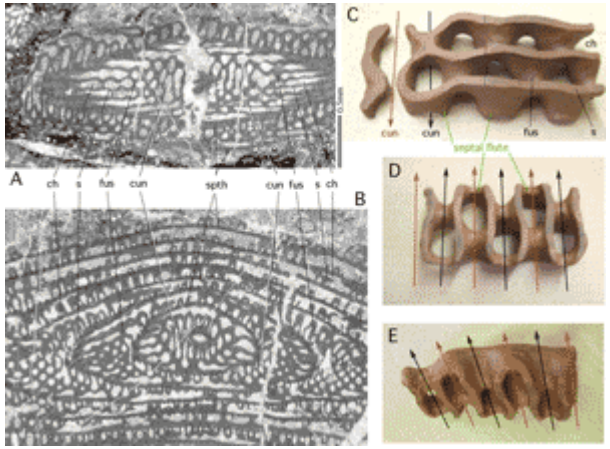


Figure 35: Cuniculi and septal fluting in *Eopolydiexodina* sp. Transmitted light micrographs. **ALLEMANN** collection, Permian, Iran.
A: shallow tangential section parallel to coiling axis. **B:** Deep transverse section parallel to coiling axis. **C-E:** plasticine model sculptured about 1945 by **M. REICHEL** (* 1896 - † 1984). **C:** Oblique peripheral view showing undivided peripheral parts of two successive chambers. Arrows point in the direction of growth. **B:** Proximal view showing cuniculi (arrows). **C:** oblique proximal view showing fluted septal face and cuniculi.
ch: chamber lumen; **cun:** cuniculus; **fus:** point of fusion of subsequent septal flutes in opposing positions; **s:** septum; **spth:** spirotheca carrying a keriotheca.

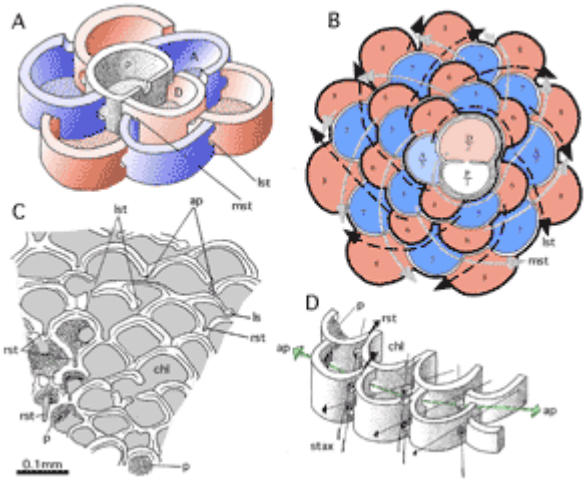


Figure 36: Development of chamberlet cycles from an auxiliary chamber in an early orbitoid, the Campanian *Lepidorbitoides minima* **H. DOUVILLÉ** from Mexico, after **AGUILAR** *et alii*, 2002.
A: stereograph of a megalospheric embryo consisting of a biconch (protoconch and deuteroconch) supplemented by a third chamber (auxiliary chamber) with

a median and two lateral stolons. Successive growth stages coloured alternately in red and blue. Lamellation omitted. Schematic, not to scale. **B:** development of chamberlet cycles. Schema, not to scale. Inner lamella omitted, outer lamella alternating in white or plain black in successive growth stages. Axes of successive stolons form overcrossing spirals (arrows). Median stolons indicated by dotted arrows, lateral stolons by black arrows. **C:** Camera lucida drawing of a slightly oblique section of the equatorial main chamberlet layer of adult growth stage showing retrovert apertures and annular passages. **D:** stereograph of adult chamberlets of two successive cycles with their crosswise-oblique stolon axes, the annular passage and their retrovert stolons. Schematic, not to scale.
A: auxiliary chamber; **D:** deuteroconch; **P:** protoconch; **X:** closing chamberlet filling up the first chamberlet annulus; **ap:** annular passage; **chl:** chamberlet lumen; **lst:** lateral stolon; **mst:** median stolon; **p:** pores; **rst:** retrovert stolons; **stax:** crosswise-oblique stolon axes.

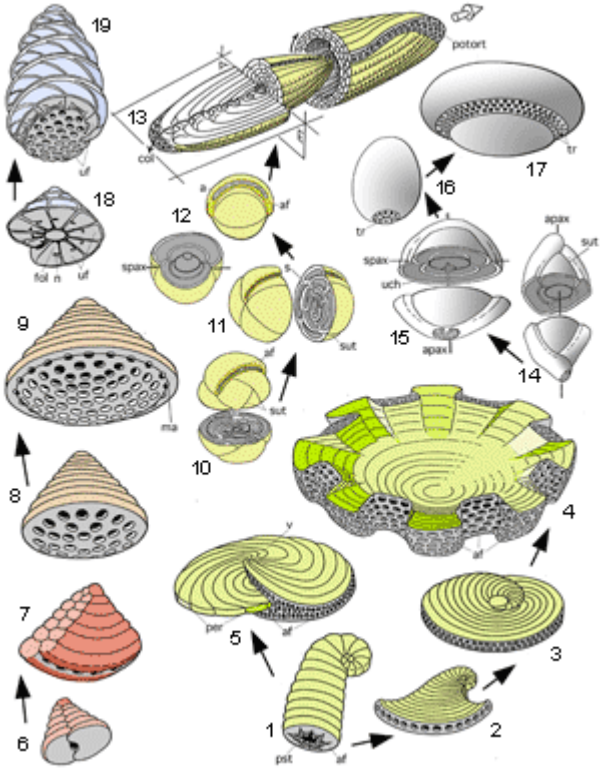


Figure 37: Chamber arrangement and apertural face. Schematic, not to scale. In part after **HOTTINGER**, 2000.
1: planispiral-spiroliniform. **2:** planispiral-evolute and flaring, peneropliform. **3:** planispiral-evolute, approaching reniform, **4:** annular-concentric, with thickened and folded margins, as in *Marginopora vertebralis*. **5:** planispiral-involute, as in *Archaias*. **6:** biserial – textulariid. **7:** biserial-cuneiform. **8:** uniserial-conical. **9:** uniserial-conical with

marginal apertures. **10:** streptospiral-involute as in *Pseudonummuloculina*. Coiling axis rotating with each chamber. **11:** streptospiral with planispiral-involute adult stage, as in *Helenalveolina*. **12:** planispiral involute. Coiling axis fixed throughout ontogeny. **13:** planispiral-fusiform: A: axial section, E: equatorial section. Black arrow: direction of growth; white arrow: direction of movement. **14:** miliolid (-quinquelocular, -trilocular), with fixed apertural axis and with coiling axis rotating in perpendicular position in respect to apertural axis. **15:** miliolid-bilocular with fixed apertural and coiling axes. **16:** unilocular-concentric, with discoidal trematophore, as in *Lacazina elongata*. **17:** unilocular-concentric with annular trematophore, as in *Lacazina compressa*. **18:** low-trochospiral, as in *Rotorbinella*. **19:** high-trochospiral, as in *Sakesaria*.
a: aperture; **af:** apertural face; **apax:** apertural axis; **col:** columella; **fol:** folium; **ma:** marginal aperture; **n:** notch; **per:** periphery; **potort:** polar totion; **pst:** peristome; **spax:** coiling axis.

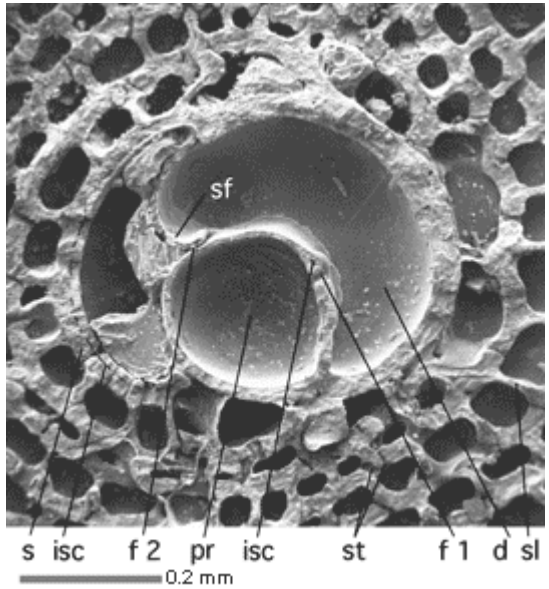


Figure 38: Deuteroconch in *Cycloclypeus carpenteri* (**BRADY**), Bikini, Pacific. Recent. SEM graph of shell split open in the equatorial plane.
d: deuteroconch; **f 1:** foramen of protoconch; **f 2:** foramen of deuteroconch; **isc:** intraseptal canal system; **pr:** proloculus; **s:** septum; **sl:** septulum; **st:** stolon (Y-shaped).

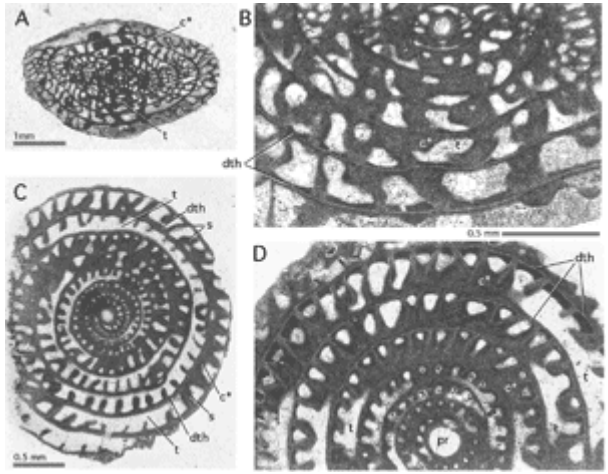
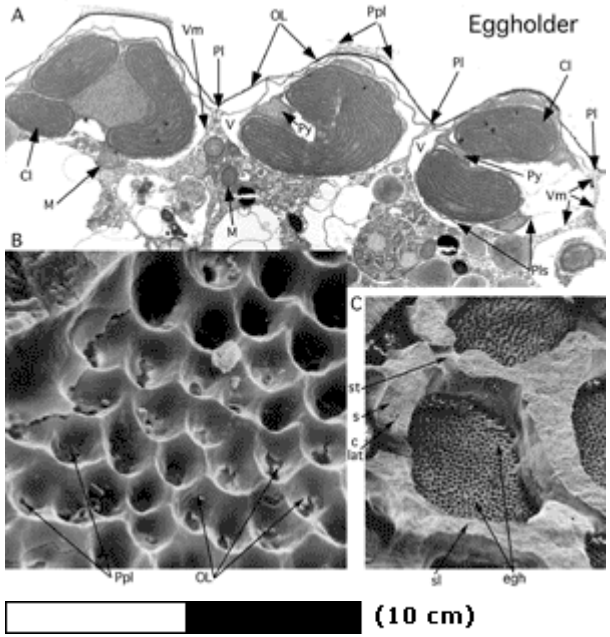


Figure 39: Diaphanotheca in *Fusulina distenta* **ROTH** et **SKINNER**, Hartville Fm., DesMoines series, Guernsay, Wyoming, Upper Carboniferous. Transmitted light micrographs.
A: slightly oblique, imperfectly centered axial section; **B:** detail of A showing diaphanotheca in axial section of adult whorls; **C:** equatorial section showing diaphanotheca extending over septal faces; **D:** detail of other specimen.
c*: choma; **dth:** diaphanotheca; **pr:** megalosphere. Note presence of some kind of flexostyle. **s:** septum; **t:** tunnel.



The magnification of each figure is in proportion to the length of the 10 cm scale bar above.

Figure 40: Eggholders harbouring the symbionts in *Heterostegina depressa* d'**ORBIGNY**. Gulf of Aqaba. Recent. **A:** TEM micrograph of section perpendicular to lateral chamber wall; biomineralized wall dissolved, organic cell walls distinctly separated by the techniques of preparation. Courtesy **S. REBER-LEUTENEGGER**. x 10,200. **B-C:** dried shell, split open in the equatorial plane. The internal surface of the lateral chamber wall bears eggholders. SEM graphs, x 5,000 and x 500. Drying strechted the organic cell walls.
Cl: chloroplast of bacillariophycean symbiont; **clat:** lateral intraseptal canal; **egh:** eggholder; **M:** mitochondria; **OL:** organic lining of host; **Pl:** plasmalemma of host; **Plp:** pore plug (see pore); **Pls:** plasmalemma of symbiont; **Py:** pyrenoid; **s:** septum; **sl:** septulum; **st:** stolon (Y-shaped); **V:** Vacuole housing symbiont; **Vm:** vacuolar membrane.

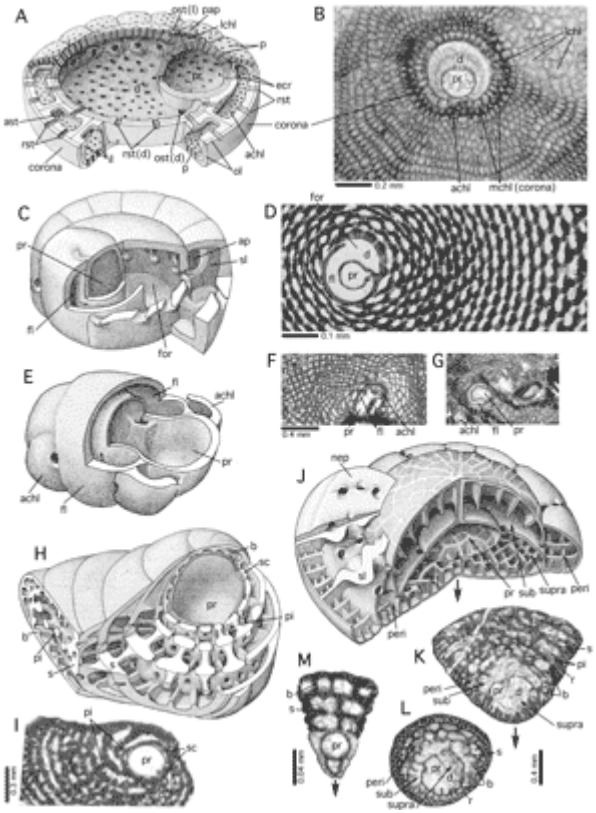


Figure 41: Embryonic apparatus.
A: *Discocyclina*, stereograph after **FERRÀNDEZ** (1999), modified. Schema, not to scale. **B:** *Discocyclina* sp., equatorial section, showing corona. Transmitted light micrograph. **C:** *Amphisorus* sp. Stereograph, schema, not to scale. **D:** *Amphisorus hemprichii* **EHRENBERG** from the Gulf of Aqaba, Red Sea. Recent. Equatorial section, transmitted light micrograph, showing flexostyle

and forecourt. **E:** *Orbitolites* sp., stereograph after **LEHMANN**, 1961, redrawn. Note the shape like a dumb-bell of the proloculus. **F-G:** *Orbitolites* sp., Lower Eocene, Pakistan, **ALLEMANN** collection. Oblique-centered sections, in approximately equatorial and axial direction, showing flexostyle constricting the proloculus. Transmitted light micrographs. **H:** *Orbitopsella* sp., stereograph showing sphaeroconch with its exoskeleton. Schema, not to scale, after **HOTTINGER**, 1967. Note the appearance of endoskeletal pillars not before the third chamber. **I:** *Orbitopsella praecursor* (**GÜMBEL**), Middle Lias, Morocco, equatorial section showing the thin proloculus wall and the sphaeroconch with its simple exoskeleton consisting of beams only. Transmitted light micrograph. **J:** Advanced orbitoliniform embryo, schematic, not to scale. Note the apex that is directed downwards (arrows) to facilitate the comparison with **HOFKER**'s drawings (1963). **K-L:** embryos of *Karsella hottingeri* **SIREL**, a Upper Paleocene form that exhibits an architecture strikingly similar to the one of Mid-Cretaceous orbitolinids. Pakistan, **ALLEMANN** collection. Transmitted light micrographs. **M:** *Sabaudia minuta* **HOFKER** Jr, embryo followed by three agglutinated chambers of the same series and presenting a simple exoskeleton. Lower Cretaceous. Note the hyaline embryo wall. The embryos are known to be formed within the mother shell and seem to have no access to grains in the environment to build their agglutinated walls.
achl: auxilliary chamberlet; **ap:** annular passage; **ast:** annular stolon; **b:** beam; **d:** deuteroconch; **ecr:** equatorial crest; **fl:** flexostyle; **il:** inner lamella; **lchl:** lateral chamberlet; **mchl:** main chamberlets; **ol:** outer lamella: **ost:** oblique stolon; **ost(d):** oblique stolon of deuteroconch; **p:** pore; **pap:** papilla; **peri:** periembryonal chamberlets; **pi:** pillar; **pr:** proloculus; **rst:** radial stolon; **rst(d):** radial stolon of deuteroconch; **s:** septum; **sc:** sphaeroconch; **sl:** septulum; **sub:** subembryonic chamber (= deuteroconch); **supra:** supraembryonic chamber.

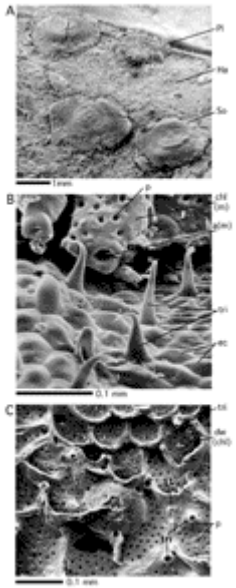


Figure 42: Epiphytic foraminifera and trichomes. Recent. Gulf of Aqaba, Red Sea. SEM graphs.
A: Epiphytes on *Halophila* leaf. **Pl:** *Planogypsina acervalis* (**BRADY**); **Ha:** surface of *Halophila* leaf with leaf hairs (trichomes); **So:** *Sorites orbiculus* (**FORSKAL**). **B:** Trichome on *Halophila* leaf and aperture in a radially-marginal position of the epiphytic *Planogypsina acervalis* (**BRADY**). **C:** Opened test of *Planogypsina acervalis* showing the inner side of the perforate, dorsal chamberlet walls, coating the overgrown trichomes of their substrate, and the dorsal part of the septal walls with stolons representing intercameral foramina.
a(m): aperture of a marginal, terminal chamberlet; **chl(m):** chamberlet of the ultimate marginal chamberlet cycle; **dw(chl):** dorsal wall of chamberlet; **ec:** epithelial cells of the *Halophila* substrate; **p:** pore; **st:** stolon; **tri:** trichome.

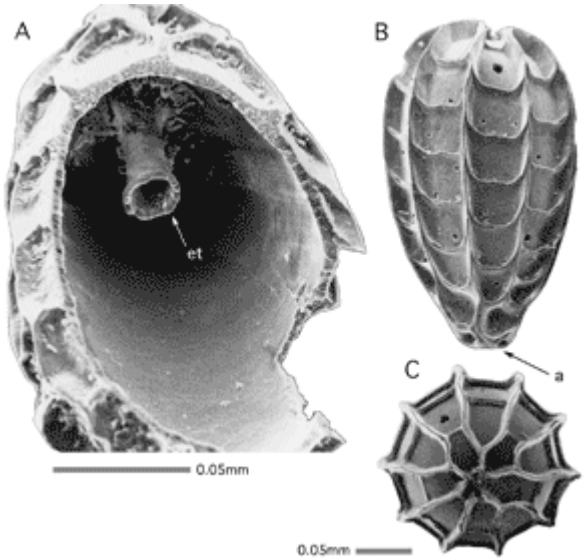


Figure 43: Endosolen in *Favulina melosquamosa* (**MCCULLOCH**), Gulf of Aqaba. Recent. SEM graphs.
A: dissected specimen, oblique aboral view; **B:** lateral view; **C:** aboral view.
a: aperture; **et:** endosolenian tube.

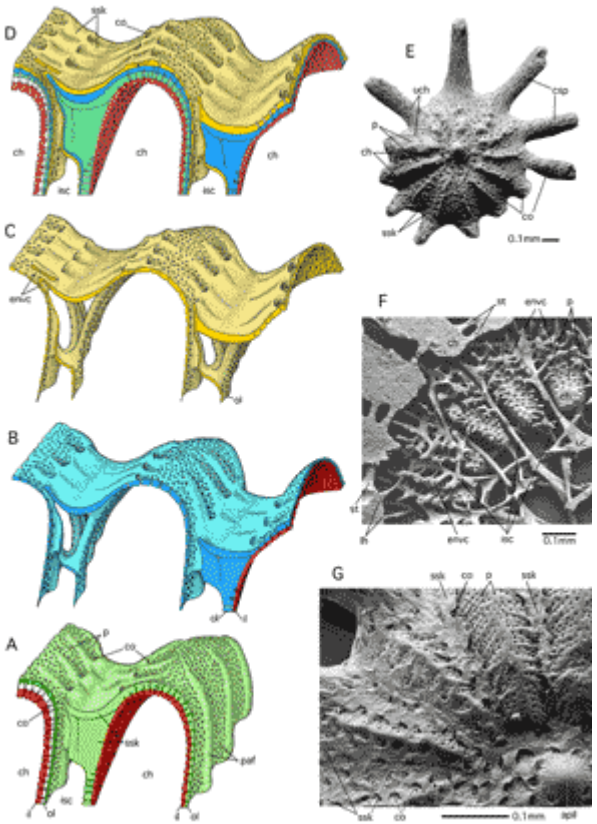


Figure 44: Enveloping canals produced by folded outer lamellas. **A-D:** Lamellae in the peripheral portion of three successive chambers. Stereograph, schematic, not to scale. **A:** ultimate and penultimate chamber: **red:** inner lamella; **green:** outer lamella of ultimate chamber, **white:** outer lamella of penultimate chamber. **B:** addition of the next chamber with an inner lamella in **red** and an outer lamella in **blue**. **C:** addition of an other chamber with its outer lamella in **yellow**. **D:** superposition of lamellas B and C over the then final chamber A after two additional growth steps. **E:** SEM micrograph of the complete test of *Calcarina defrancii* d'**ORBIGNY**, ventral view, showing distribution of canal orifices over all the test including the canaliferous spines. **F:** SEM micrograph of an epoxy resin cast of the shell cavities in *Calcarina gaudichaudii* d'**ORBIGNY** cut in a direction perpendicular to the axis of the spiral shell, ventral view; **G:** detailed SEM micrograph of the ventral shell surface of *C. gaudichaudii*. Calcarinas from Keij Island, Indonesia. Recent. After **HOTTINGER** and **LEUTENEGGER**, 1980. **apil:** axial pile of lamellae; **ch:** chamber and chamber lumen; **co:** canal orifice; **csp:** canaliferous spine; **envc:** enveloping canal; **isc:** intraseptal space or canal; **il:** inner lamella; **lh:** loop-hole; **ol:** outer lamella; **p:** pore; **paf:** perforate part of apertural face; **ssk:** supplemental skeleton; **st:** stolon; **uc:** umbilical canal network; **uch:** ultimate chamber suture, chamber walls broken off.

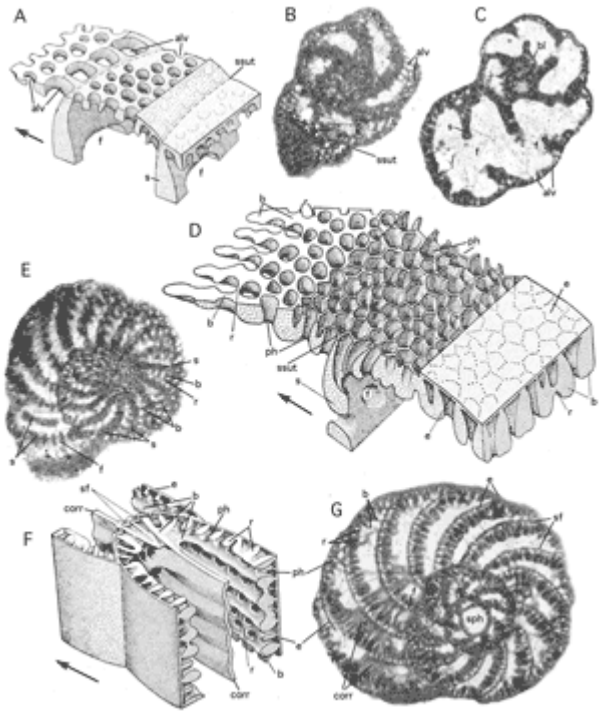


Figure 45: Alveolar exoskeleton and polygonal network.
A-C: simple alveolar layer in *Everticyclammina virguliana* (**KOECHLIN**), Mechra Klila, Northeastern Morocco, Uppermost Jurassic. **A:** stereograph, schematic, not to scale. **B:** tangential section. Note the large size of the alveoles in a postseptal position. **C:** para-equatorial, non-centered section showing septa and the basal coat at the bottom of the chamber, resembling a basal layer. **E-G:** polygonal network in Spirocyclinidae. **E:** *Choffatella tingitana* **HOTTINGER**, megalospheric generation, in tangential section near to the equatorial plane. Note the clear differentiation of beams and rafters. **D:** stereograph of spirocyclinid polygonal network. Note the curved pigeon holes in preseptal position which in axial section might be mistaken for foramina. **F-G:** extension of beams into a corrugated sheet that replaces endoskeletal pillars in Hottingertidae. **F:** stereograph representing a part of an axial section. Not to scale. **G:** *Alveosepta powersi* (**REDMOND**), Northeastern Morocco, Upper Jurassic. Equatorial section of megalospheric specimen.
alv: alveoles; **b:** beam; **bl:** basal layer; **corr:** corrugated median extension of beams; **f:** foramen; **ph:** pigeon holes; **s:** septum; **sf:** supplementary foramina; **sph:** sphaeroconch; **ssut:** septal suture. **Arrows:** direction of growth. After **HOTTINGER**, 1967.

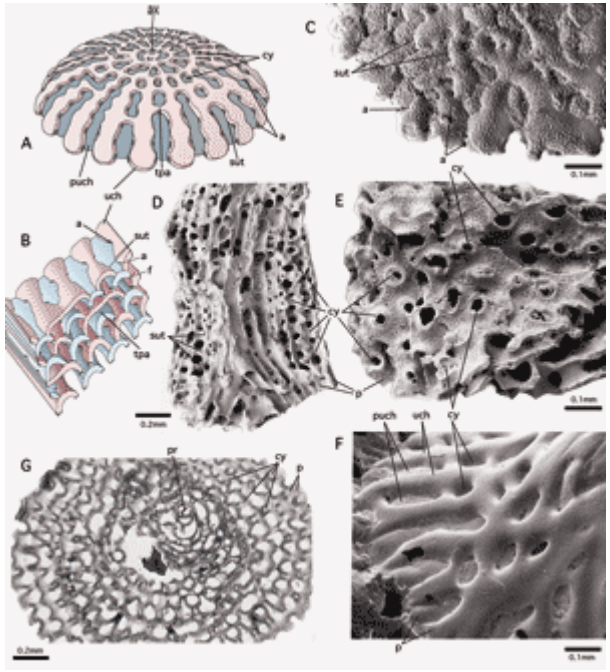


Figure 46: Expanse chambers and calyces.
A: Sketch of ultimate and penultimate expanse chambers, not to scale. **B:** A cut-out portion of five successive expanse chambers, cut in an oblique direction with respect to the shell axis, schematic, not to scale. Lamellation of walls omitted. **C:** Ultimate and penultimate expanse chambers in *Planogypsina squamiformis* (**CHAPMAN**). Gulf of Aqaba, Red Sea; Recent. SEM graph. **D-G:** Expanse chambers with calyces in *Miniacina miniacea* (**PALLAS**), Gulf of Aqaba, Red Sea; Recent. **D-F:** SEM graphs, **G:** thin section in transmitted light. **D:** broken surface perpendicular to the axis of a branch of the arborescent shell: the expanse chambers are grouped around tubular extensions of the peristomes of earlier chambers. **E:** a fragment of shell showing the inner surfaces of two successive expanse chambers. Note the alternating arrangement of the calyces. **F:** radial spreading of ultimate expanse chamber at the foot of an arborescent shell, thus enlarging the shell's surface of attachment. **G:** centered section near and parallel to the surface of attachment, so cutting the latest, outermost expanse chambers at diminishing angles.
a: aperture; **ax:** shell
axis; **cy:** calyx; **p:** pore; **pr:** proloculus; **puch:** penultimate expanse chamber; **sut:** suture of expanse chamber; **tpa:** tubular passage connecting parts of expanse chamber; **uch:** ultimate expanse chamber.

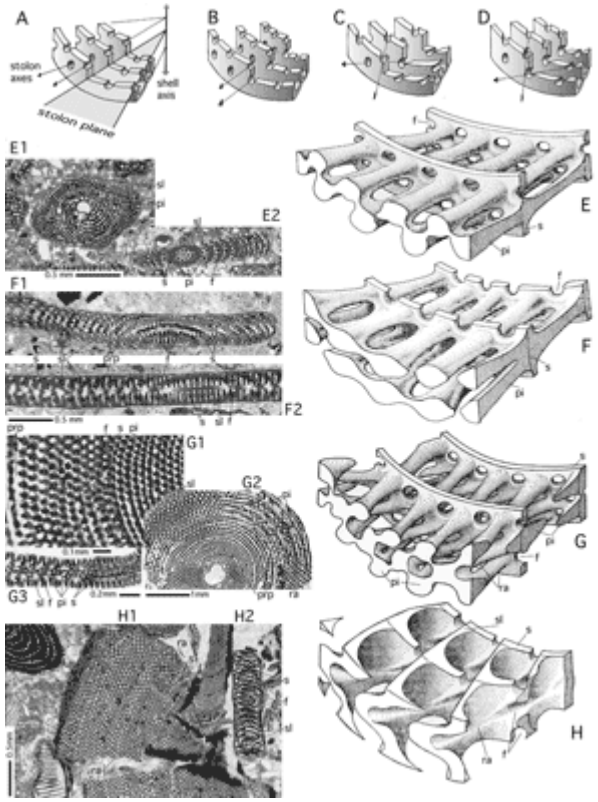


Figure 47: Endoskeletal patterns in discoidal shells.
A-D: disposition of apertural axes. **A:** radial axes alternating in radial position from one stolon layer to the next. This is the most common disposition in imperforate forms with annular stages of growth. **B:** radial axes superposed in radial position on all stolon planes. **C:** crosswise-oblique stolon axes alternating in radial position from one stolon plane to the next. **D:** crosswise-oblique stolon axes superposed on all stolon planes. This pattern characterizes all members of the orbitolitid family. Schematic, not to scale. **E-H:** all endoskeletal elements are disposed in accordance with the basic patterns of the foraminal axes: **E** corresponds to pattern A, **F** to pattern B, **G** to pattern C and **H** to pattern D. Stereographs after **HOTTINGER**, 1967. Schematic, not to scale. In reality, the patterns are often disturbed by intercalary elements generated as the diameter of the annuli increases during growth. This maintains on the apertural face the mean distances between apertures and their mean diameter constant during ontogeny. Examples: **E1-2:** *Pseudotaberina malabarica*, megalospheric generation, from Iran. Middle Miocene. **E1:** oblique-centered section of spiral-involute stage showing radial disposition of pillars. Laterally, there is a layer of short septula. **E2:** a transverse section tangential to a septum shows the alternating disposition of the foramina and the pillars. **F1-2:** New genus (possibly related to *Pastrikella*) from the Pyrenean Upper Cretaceous in Northern Spain. The endoskeleton consists only of septula. There is but one median annular preseptal passage and it occupies the total radial extension of the annular chamber. There are only two planes of stolons. **F1:** an oblique section at a low angles with respect

to the equatorial plane shows the radial disposition of the apertural axes and of the septula. **F2:** a transverse section parallel to the shell axis shows that the stolon axes on the two stolon planes are superposed. **G1-3:** *Amphisorus* from Rottnest Island near Perth, Australia. Recent. **G1:** the detail of an equatorial section demonstrates the crosswise-oblique disposition of the pillars on neighboring stolon planes. **G2**, an equatorial section, demonstrates that pillars are restricted to the equatorial zone of the disc. **G3:** a transverse section parallel to the shell axis and tangential to an annular septum shows the disposition of the median foramina and pillars altermating in radial position on successive stolon planes. They are flanked by two annular preseptal passages separating them from a lateral layer of septula subdividing the annular chamber. **H1-2:** *Orbitolites* spp. from the region of Tremp, Lerida prov., Northern Spain. Pyrenean Lower Eocene (Ilerdian). **H1:** the comparatively regular disposition of the ramps in sections parallel to the equatorial plane reveals their superposition in consecutive stolon planes. **H2:** in the transverse section parallel to the axis of the shell this superposition is clearly visible where the section is tangential to an annular septum.
Abbreviations: **b:** beam; **f:** foramen; **pi:** pillar; **prp:** preseptal space; **ra:** ramp; **s:** septum; **sl:** septulum.

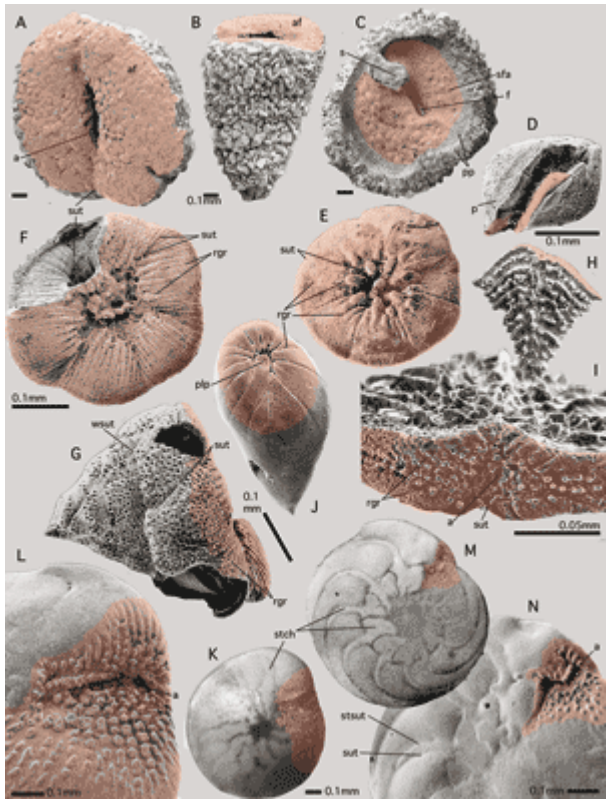


Figure 48: Faces (coloured red) in biserial and spiral forms. SEM graphs (if not specified otherwise) of specimens from the Gulf of Aqaba, Red Sea. Recent.

A-C: *Textularia* aff. *goesi* **CUSHMAN**, apertural and lateral views of intact specimens and frontal view of broken specimen showing septal face. Note the smooth surfaces characteristic of the faces of many agglutinated forms. **D-E:** *Discorbinoides* sp. A in **HOTTINGER** *et alii*, 1993. Plastogamic pair and plastogamic umbilical face with radial grooves. **F-G:** *Glabratellina* sp. A in **HOTTINGER** *et alii*, 1993. Ventral view showing plastogamic ventral face with radial grooves and lateral view showing shell whorls with their sutures. **H-I:** *Bolivinella elegans* **PARR**, a lamellar-perforate, biserial form with known plastogamic reproduction, that has radial grooves on its face. **J:** *Floresina spicata* (**CUSHMAN** et **PARKER**) has a smooth face with few radial grooves and in addition grooved septal sutures. A (plastogamic?) plate covers the narrow umbilicus. As yet, plastogamy has not been observed in vivo in this species. **K-L:** *Amphistegina lobifera* **LARSEN**, Megalospheric specimen in incident light micrograph, ventral view and detail of apertural face. Note the extension of the ornamented surface for a notable distance over peripheral-ventral parts of the previous whorl. **M-N:** *Amphistegina bicirculata* **LARSEN**, megalospheric specimen in incident light micrograph, ventral view and detail of apertural face. Note comparatively much smaller ornamented surface corresponding to lower water energy in its deeper habitat.
a: aperture; **af:** apertural face; **f:** foramen; **p:** pore; **plp:** plastogamous (?) plate; **pp:** parapore; **rgr:** (plastogamous) radial grooves; **sfa:** septal face; **stch:** stellar chamberlet; **stsut:** stellar suture; **sut:** (chamber) suture; **wsut:** whorl suture.

Figure 49: Equitant chambers in *Frondicularia* sp. from the Prerif, Northwestern Morocco, Lower Miocene. Transmitted light micrograph of section in the sagittal plane of a microspheric specimen. Note the denticulate margin of the single, stellar foramen in terminal position (**f**) and the extremely fine perforation of the septal wall that is characteristic of most nodosariids.

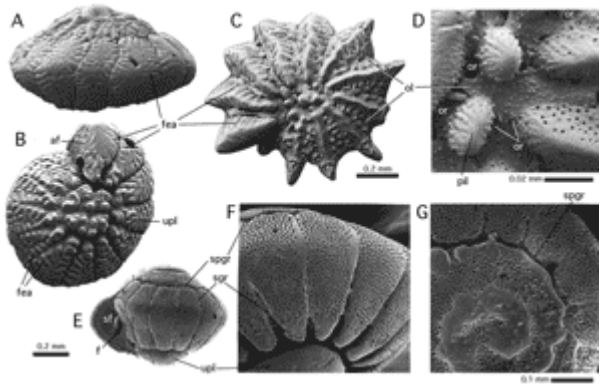


Figure 50: Feathered grooves. All specimens figured as SEM graphs. **A-B:** *Ammonia beccarii* (**LINNÉ**), Adriatic Sea, Recent. Peripheral and oblique - umbilical views. Note the ridges on the apertural face that initiate the feathering when the next chamber is added during ontogeny. **C-D:** *Neorotalia calcar* (d'**ORBIGNY**), Keij Island, Indonesia. Recent. Ventral view of an entire specimen and detail of a ventral feathered groove covered by a folded outer lamella. Note the imperforate nature of the cover and the orifices of the canal system. Compare: enveloping canal systems in Fig. 44. **E-G:** Unfeathered grooves in *Ammonia ikebei* (**INOUE** et **NAKASEKO**), Eastern Kalimantan, Borneo, Upper Miocene. Peripheral view of entire specimen and details in oblique-umbilical and in dorsal views. Note the hemicircular attachment of the septal flap and the undivided umbilical plug that correspond to unfeathered septal grooves.
af: apertural face; **f:** foramen; **fea:** feathered grooves; **ol:** (folded) outer lamella covering a septal groove that is converted to an interlocular space; **or:** canal orifice; **pil:** pile; **s:** septum; **sgr;** septal groove (unfeathered); **spgr:** spiral groove (unfeathered); **upl:** umbilical plug.

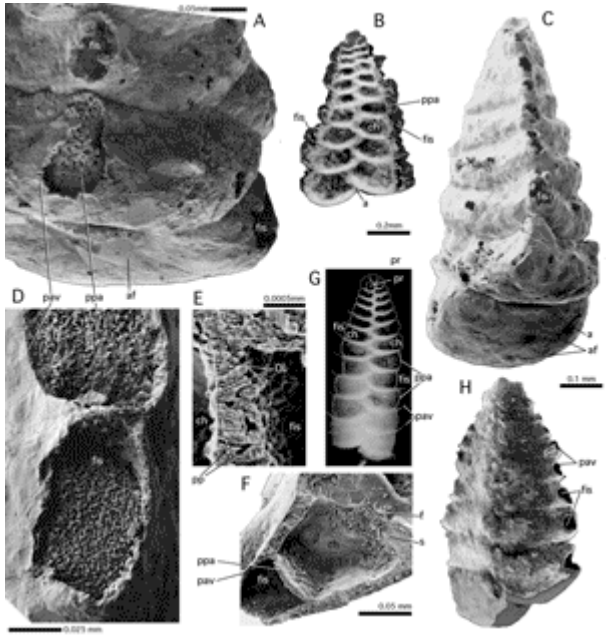


Figure 51: Fistulose chamberlets. All specimens from the Gulf of Aqaba, Red Sea, Recent.
A-C: *Sahulia kerimbaensis* (**SAID**). **A:** Detail of an edge view, SEM graph; **B:** side view, X-ray graph, black background removed. Note the narrowness and the irregularity of the fistulose chamberlets in this species. **C:** edge view, SEM graph. **D-H:** *Spirotextularia floridana* (**CUSHMAN**). **D:** paraporous partition separating the chamber lumen from a fistulose chamberlet. SEM graph. **E:** Detail of sectioned paraporous partition. SEM graph. Note the organic lining that closes off the parapores from the chamber lumen. SEM graph. **F:** Shell fragment broken in a direction perpendicular to the shell axis, showing paraporous partition between the chamber lumen and the fistulose chamberlet. SEM graph. **G:** Lateral view, X-ray graph. **H:** lateral view of an entire specimen. SEM graph. Note the spiral arrangement of the nepionic chambers.
a: aperture; **af:** apertural face; **ch:** chamber lumen; **f:** foramen; **fis:** fistulose chamberlet; **OL:** organic lining; **pp:** parapore; **ppa:** paraporous partition; **pr:** proloculus; **pv:** pavement; **s:** septum.

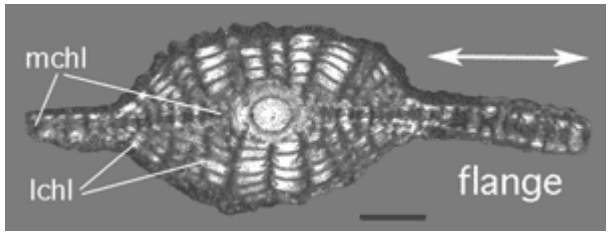


Figure 52: The flange (double arrow) in *Nephrolepidina* sp., axial section, transmitted light. Oligocene, Sarawak, Borneo.

lchl: lateral chamberlets; **mchl:** median chamberlet layer. Scale bar 0.2 mm.

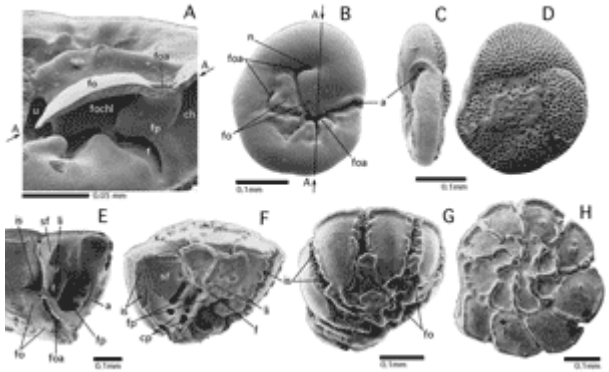


Figure 53: The folium and its apertures. All specimens from the Gulf of Aqaba, Red Sea, Recent. SEM graphs.
A-D: *Rosalina bradyi* (**CUSHMAN**). **A:** detail of dissected specimen, oblique-ventral view. The approximate position of the breakage surface (arrows A-A) is indicated by the line A-A in Fig. B. **B:** ventral view showing the folium at its maximum development, with anterior and posterior apertures. **C-D:** peripheral and dorsal views. Note the restriction of the perforation to the dorsal surface of the shell, an indication that the face extends from the umbilical side of the shell over its periphery. **E-H:** *Asterorotalia gaimardi* (d'**ORBIGNY**). **E-F:** dissected specimens showing details of advanced umbilical architecture covered by the folia: foraminal and coverplates (compare Fig. 34). **G:** oblique-ventral view showing the folia that cover the ventral part of the interlocular space. **H:** dorsal view showing the spiral arrangement of the chambers.
a: aperture; **ch:** chamber lumen; **cp:** coverplate; **f:** foramen; **fo:** folium; **foa:** foliar aperture; **fochl:** foliar chamberlet lumen; **fp:** foraminal plate; **is:** interlocular space; **li:** lip (of foramen); **n:** notch; **sf:** septal flap; **u:** umbilicus.

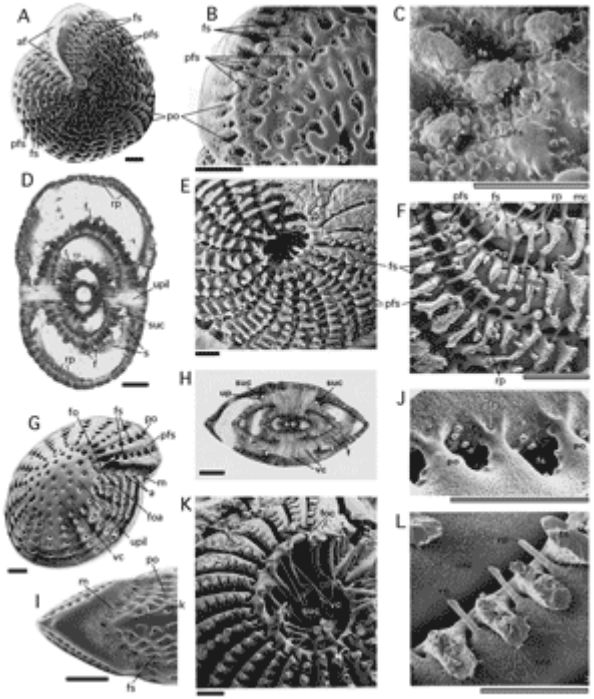


Figure 54: Fossette, parafossette, ponticulus and retral process in advanced elphidiids from the Gulf of Aqaba, Red Sea. Recent. SEM graphs except D and H.
A-F: *Elphidium striatopunctatum* (**FICHTEL** et **MOLL**). **A:** lateral (umbilical) view of the surface of the shell. **B:** detail showing the orifices of the canal system. Note the heavy spiking of the orifices, a device to fend off inedible particles such as diatom frustules. **C:** the detail of an orifice of a parafossette. Note its alignment with the axis of the adjacent ponticulus. **D:** axial section of megalosperic specimen, transmitted light micrograph. Note the row of foramina at the base of the chamber and the row of retral processes in the chamber roof. **E:** epoxy resin cast of the cavities of the shell showing the narrow spiral of the umbilical canal and the double row of fossettes and parafossettes representing the septal interlocular space. **F:** detail of a cast showing the disposition of fossettes and parafossettes and their connection to the intraseptal canal system. **G-L:** *Elphidium craticulatum* (**FICHTEL** et **MOLL**). **G:** oblique-peripheral view of entire shell. **H:** axial section of megalospheric specimen. Transmitted light micrograph. Note the single row of foramina at the bottom of the chamber and the broad umbilical pile with its funnels. **I:** apertural face showing the masked apertures. Note the imperforate keel, an important specific character. **J:** detail of G: the orifices of the fossettes in the last chamber alternate with tiny parafossettes. These disappear when they are covered by subsequent secondary lamellation in later stages of growth. **K:** epoxy resin cast showing umbilical cavities including the foliar chamberlets at the tips of the alar prolongation of the chamber. The foliar chamberlets are transformed during ontogeny into a spiral umbilical canal. **L:** epoxy resin cast showing detail of septal architecure: the alternation of retral processes and fossettes. Note the

tiny pores on the cast of the main chamber lumen and the traces of the spikes on the walls of a fossette.
a: aperture; af: apertural face; **f:** foramen; **fo:** folium; **foa:** foliar aperture; **foc:** foliar chamberlet; **fs:** fossette; **k:** keel; **m:** mask; **mc:** main chamber lumen; **pfs:** parafossette; **po:** ponticulus; **rp:** retral process; **s:** septum; **suc:** spiral umbilical canal; **upil:** umbilical pile; **vc:** vertical canal (funnel). Scale bars: 0.1 mm, double scale bars: 0.05 mm.

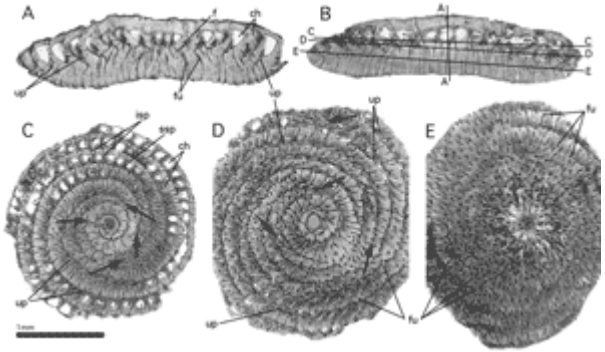


Figure 55: An umbilical architecture dominated by funnels: *Dictyokathina simplex* **SMOUT**, megalospheric specimens from Qatar, Paleocene. Transmitted light micrographs.
A: subaxial section showing funnels in their longitudinal extension. **B:** transverse section near the axis of the shell with the positions of sections A & C-D indicated. **C-E:** sections more or less perpendicular to the axis of the shell showing the vast umbilical area crowded with funnels. Note the chamber arrangement in multiple spirals, The start of supplementary spirals is indicated by **arrows**. The material does not allow resolution of the question: is the first chamber of a supplementary spiral fed from a foramen or from a canal?
ch: chamber lumen; **f:** foramen; **fu:** funnel (vertical canal); **isp:** intraseptal interlocular space; **ssp:** spiral interlocular space; **up:** umbilical plate.

The magnification of the figure is in proportion to the length of the 10 cm scale bar above.

Figure 56: The Golgi apparatus and mitochondria in the cytoplasm of *Alveolinella quoyi* (d'**ORBIGNY**) from the Maldive Islands, Indian Ocean. Transmission electron micrograph, x 50,000. Courtesy **S REBER-LEUTENEGGER**. **G:** Golgi apparatus with its cisternae (**cist**); **M:** mitochondrium with its cristae (**cr**).

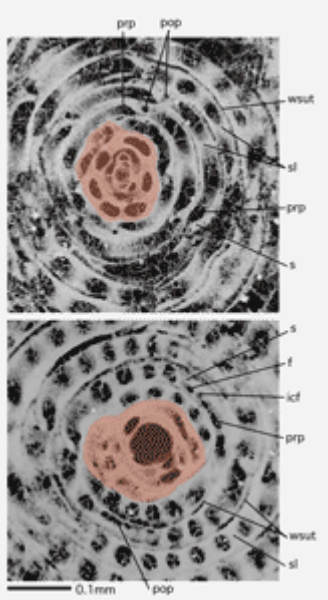


Figure 57: Glomerulus (coloured) in *Glomalveolina lepidula* (**SCHWAGER**) from Tremp, Northern Spain, Ilerdian. Approximately equatorial section with small, ? microspheric proloculus and axial section with large, ?megalospheric proloculus. Incident light.
f: foramen; **icf:** intercalary foramen; **pop:** postseptal passage; **prp:** praeseptal passage; **s:** septum; **sl:** septulum; **wsut:** whorl suture (enlarged by slight deformation).

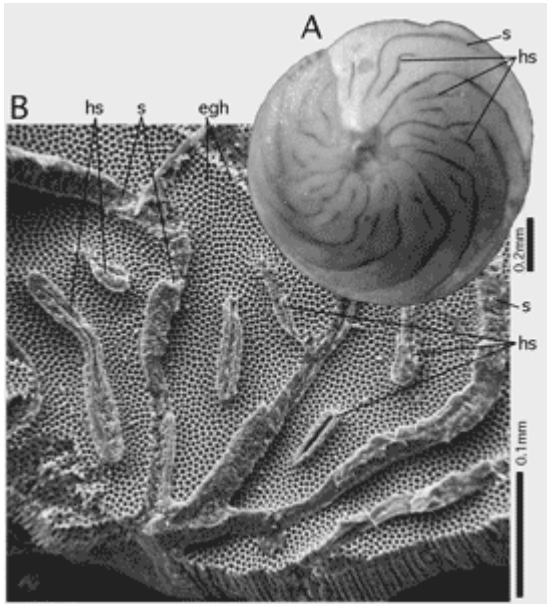


Figure 58: Hemiseptula in *Amphistegina lessonii* d'**ORBIGNY** from the Gulf of Aqaba, Red Sea. Recent.
A: the dorsal surface of a megalospheric specimen. Incident light. **B:** the inner surface of a fragment of dorsal chamber walls showing septa and hemiseptula broken at a short distance from the level of the eggholders. Note the three-layered texture of the septa (a primary bilamellar wall plus a septal flap) and the two-layered nature of the hemiseptula that results from the folding of the inner lamella. SEM graph.
egh: eggholder; **hs:** hemiseptula; **s:** septa.

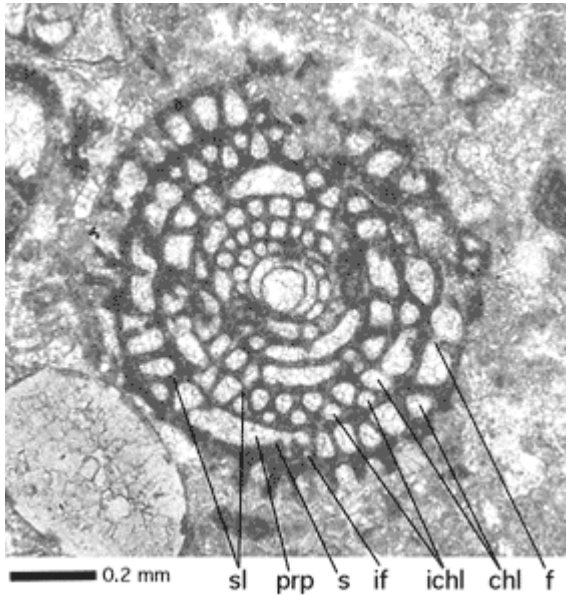


Figure 59: Intercalary chamberlets in *Borelis curdica* (**REICHEL**). Qum Basin, Iran. **ALLEMANN** collection 229. Lower Miocene. Axial section.
chl: chamberlet; **f:** foramen; **ichl:** intercalary chamberlet; **if:** intercalary foramen; **prp:** preseptal passage; **s:** septum; **sl:** Y-shaped septulum.

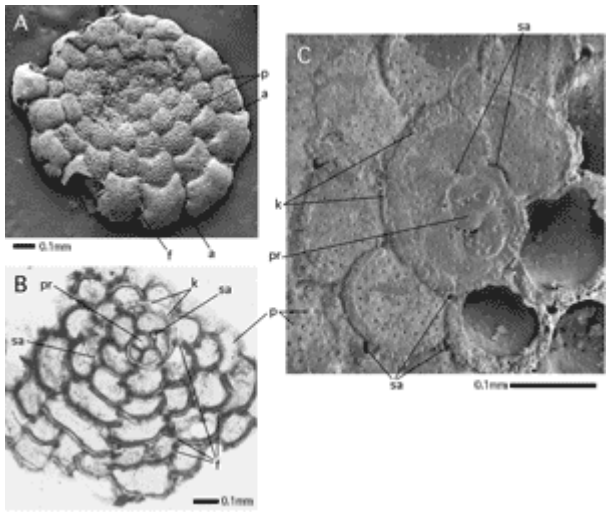


Figure 60: Surface of attachment with supplementary apertures in *Planorbulina mediterranensis* d'**ORBIGNY**. Elba Island, Mediterranean. Recent.
A: Free surface with apertures in subperipheral position. SEM graph. **B:** Equatorial section showing the nepionic, keeled spiral chambers

followed by early chamberlet cycles with their oblique foramina and supplementary apertures where the section passes immediately below or within the attached chamber walls. Note the straight septa between the proconch and the two following chambers forming together a triconch. Transmitted light micrograph. **C:** Detail of surface of attachment with its tiny supplementary apertures in sutural position. Note the keeled nepiont. SEM graph.
a: aperture; **f:** foramen; **k:** keel of the nepiont; **p:** pore; **pr:** proloculus; **sa:** supplementary aperture.

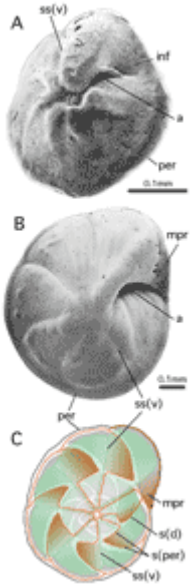


Figure 61: Infundibulum and marginal prolongation.
A: *Neoeponides bradyi* (**LE CALVEZ**), oblique-ventral view showing infundibulum. SEM graph; Gulf of Aqaba, Red Sea; Recent. **B:** *Eponides repandus* (**FICHTEL** et **MOLL**), ventral view showing marginal prolongation. SEM graph; Gulf of Aqaba, Red Sea; Recent. **C:** Schematic drawing showing position of marginal prolongations in respect to ventral and dorsal test morphology in the last whorl of *Eponides repandus*.
Gray: dorsal view with raised sutures; **red:** outline of chamber walls at level ventrally below periphery; **green:** ventral ouline of chambers below level of marginal prolongation.
a: aperture; **inf:** infundibulum; **mpr:** marginal prolongation; **per:** (imperfotate) periphery; **s(d):** (oblique) septum (as seen in dorsal view); **s(per):** position of septum at level of periphery; **ss(v):** (radial) septal suture in ventral view.

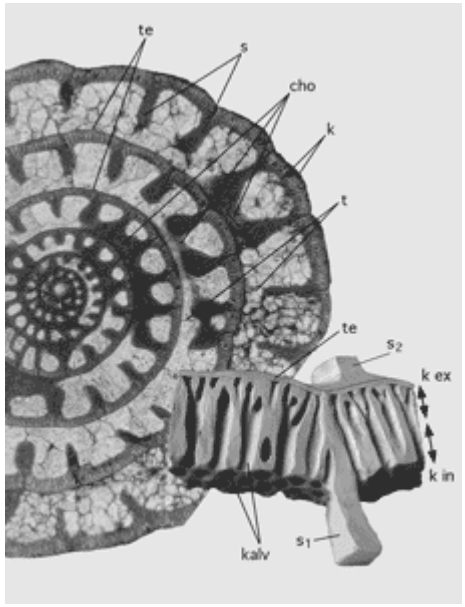


Figure 62: Keriotheca (double arrow) in equtorial section of unidentified *Triticites* and as plasticine model by **M. REICHEL** (unpublished, modified).
cho: choma; **kalv:** keriothecal alveoles; **k ex:** extern keriotheca; **k in:** intern keriotheka; **s:** septum; **s_1:** septum belonging to whorl bearing the keriotheka; **s_2:** septum of following whorl; **te:** tectum.

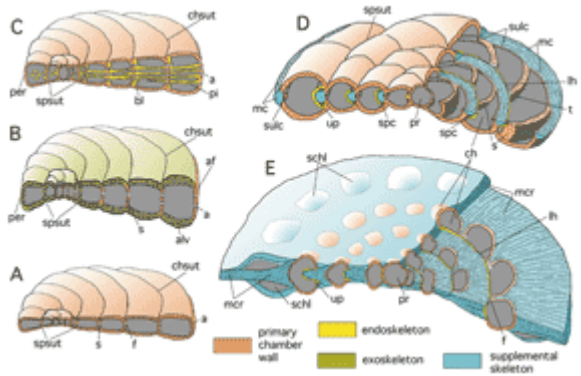


Figure 63: Comparison of foraminiferal skeletons. Schematic, not to scale. Lamellation, perforation and canal orifices omitted.
A: a planispiral-evolute shell without skeletal structures, composed of simple primary chamber walls with multiple apertures, such as that of *Peneroplis*. **B:** a planispiral-evolute shell with an alveolar exoskeleton, such as *Pseudocyclammina*. **C:** a planispiral shell with a pillared endoskeleton such as *Archaias*. Note that in the axial sections of shells with peneropliform, flaring

chambers the periphery of the shell and the apertural face are on opposite sides. Consequently, the pillars extending from chamber bottom to chamber roof appear in the axial plane on the side cutting the apertural face as longitudinal and on the other side cutting the periphery as more or less perpendicular sections. **D:** a spiral shell with a supplemental skeleton restricted to the periphery of the shell, as in nummulitids with a marginal cord. **E:** a spiral shell with an enveloping canal system and a marginal crest as in *Pellatispira*. Note the primary lateral chamber walls "emerging" from the supplemental skeleton. These primary chamber walls are covered by secondary lamellae but are perforated in continuation of the primary bilamellar wall. Therefore they are not a part of the supplemental skeleton. The supplemental chamberlets have perforate lateral walls but do not communicate directly with the spiral chambers by retral stolons. They are fed by canal orifices.
a: aperture; **af:** apertural face; **alv:** alveole; **bl:** basal layer; **ch:** chamber; **chsut:** chamber suture; **f:** foramen; **lh:** loophole; **mc:** marginal cord; **mcr:** marginal crest; **per:** periphery; **pi:** pillar; **pr:** proloculus; **s:** septum; **schl:** supplemental chamberlet; **spc:** spiral canal; **spsut:** spiral suture; **sulc:** sulcus; **t:** tunnel; **up:** umbilical plate.

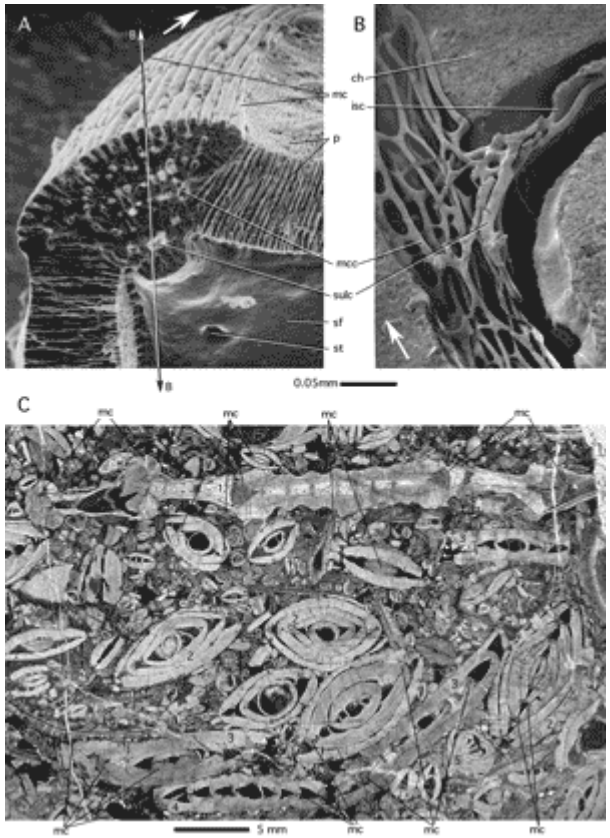


Figure 64: Marginal cord in nummulitids.
A-B: *Assilina ammonoides* (**GRONOVIUS**), Recent, Gulf of Aqaba, Red Sea. SEM graphs after **HOTTINGER**, 1977. **A:** Detail of marginal cord in a shell broken in the axial plane. Double arrow B - B indicates the approximate position of the cut in the cast of Fig. B. **B:** Detail of marginal cord in an epoxy resin cast that was cut approximately in the equatorial plane (as indicated in Fig. A), showing canal and chamber lumina after dissolution of shell. White arrows indicate direction of growth. **C:** Nummulitic limestone from Steinbach, Einsiedeln, Swiss Helvetic Alps, Lower Eocene (Cuisian). Transparent light micrograph of section perpendicular to bedding plane. **1:** *Assilina* sp. of *A. ammonea-praespira* phyletic line, with particularly large and prominent marginal cord; **2:** *Nummulites* spp.; **3:** *Assilina* sp. of *A. spira* phyletic line; **4:** *Assilina* sp. of *A. exponens* phyletic line; **5:** *Asterigerina* cf. *rotula* (**KAUFMANN**): no marginal cord.
ch: chamber lumen; **isc:** intraseptal canal system; **mc:** marginal cord; **mcc:** marginal cord canals; **sf:** septal flap; **st:** stolon; **sulc:** sulcus canal.

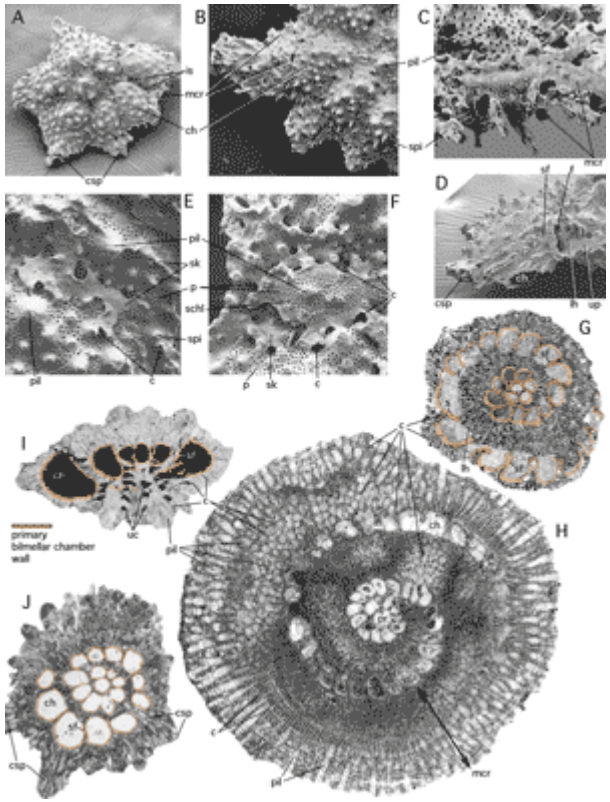


Figure 65: Supplemental skeletons including marginal crests.
A-G: *Pellatispira* group *provalei* **YABE**. **H:** *P. fulgeria* **WHIPPLE**. Both species from Kalimantan, Borneo, Indonesia. Middle-Upper Eocene. **I-J:** *Calcarina* sp., Kutei basin, Kalimantan. Pleistocene. **A-D:** SEM micrographs. **G-J:** transmitted light micrographs of oriented thin sections of free specimens. **A:** the free

nepiont shows early spiral chambers not yet covered by a supplemental skeleton. An uncovered open interlocular space remains between the ultimate and penultimate chambers. **B:** detail of lateral view of a free nepiont revealing the early presence of canaliculate spines in the first volution of the spiral chambers and the modest extent of the marginal crest at this stage of growth. **C:** peripheral view of the margin of the second whorl. Note the strong radial spikes that support the thin imperforate walls of the marginal crest. **D:** septal face in oblique-peripheral view: the septal flap is reduced to a small area above the foramen. **E:** a lateral, flying cover of the interlocular space, with canal orifices at its margins, is produced by a free fold of an outer lamella and represents thus a primary element of the supplemental skeleton. **F:** in later growth stages, a first imperforate cover of the interlocular space may be bridged by supplementary chamberlets with a perforate, bilamellar wall. **G:** equatorial section. The primary bilamellar walls of the spiral chambers are coloured. All uncoloured constituents of the shell are part of the supplemental skeleton. **H:** Extreme development of the supplemental skeleton as a broad marginal crest covered with piles that are flanked by the canals of an enveloping system. **I:** the axial section of a trochospiral shell demonstrates the complex pattern of the umbilical cavities between umbilical piles of lamellae. The primary bilamellar walls of the spiral chambers are coloured. **J:** a section perpendicular to this axis of coiling shows that canalicular spines grow outward from the supplemental skeleton that envelops the primary bilamellar (coloured) wall of the spiral chambers.
Abbreviations: **a:** aperture; **c:** canals, canal orifices; **ch:** (spiral) chamber; **chl:** (supplemental) chamberlet; **csp:** canaliculate (pseudo)spine; **f:** foramen; **is:** intraseptal interlocular space; **lh:** loophole; **mcr:** marginal crest; **p:** pore; **pil:** pile (of lamellae); **pr:** proloculus; **s:** septum; **schl:** supplemental chamberlet; **sf:** septal flap; **sk:** supplemental skeleton; **spi:** spike; **uc:** umbilical cavity system; **up:** umbilical plate.

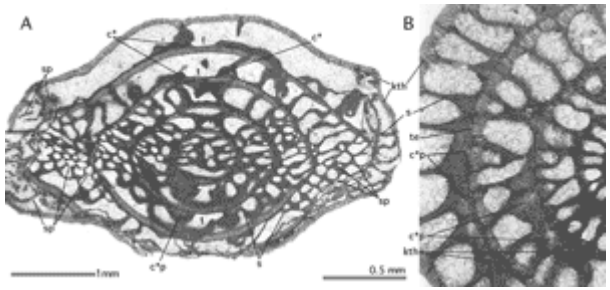
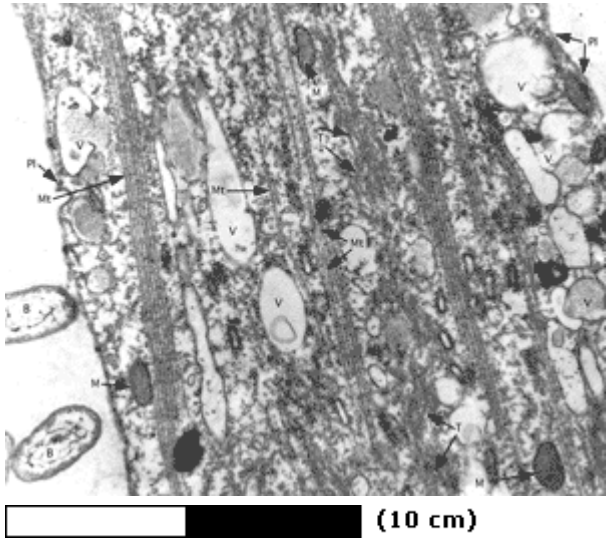


Figure 66: Septal and chomatal "pores" in *Triticites plummeri*, Graham Fm., Texas, Permian. Transmitted light micrographs.
A: subaxial section; **B:** details in equatorial section. Both pore-like features have nothing in common with true pores. Septal pores are tiny multiple foramina. The nature of chomatal pores, a wall texture particular to fusulinids, is not understood at present.
c: choma; **c*p:** chomatal "pores"; **kth:** keriotheka; **sp:** septal "pores". **t:** tunnel; **te:** tectum.



The magnification of the figure is in proportion to the length of the 10 cm scale bar above.

Figure 67: Microtubules (Mt) and tubulin paracrystals (T) in canal ectoplasm of *Assilina ammonoides* (**GRONOVIUS**). TEM micrograph, courtesy **S. REBER-LEUTENEGGER**, x 24,000.
B: bacteria; **M:** mitochondria; **Mt:** microtubule; **Pl:** plasmalemma; **T:** tubulin paracrystals; **V:** vacuoles with or without fibrillar content (waste products?).

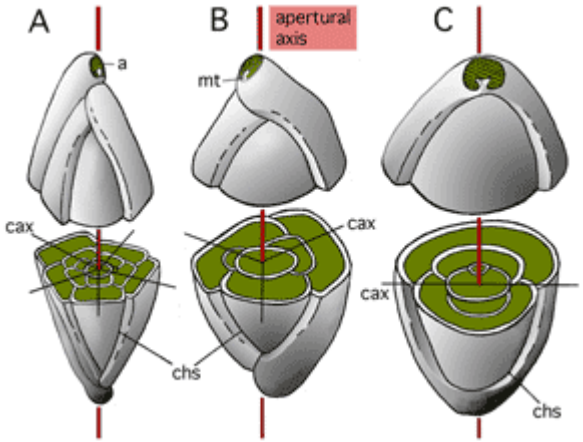


Figure 68: Milioline coiling. Schematic, not to scale. Note the coiling mode: only two chambers per whorl. Chamber lumina green, coiling axes black. Foramina aligned in the apertural axis (red).
A: quinqueloculine mode of coiling: for each new chamber the coiling axis rotates 72° around the apertural axis. **B:** triloculine mode of coiling: for each new chamber the coiling axis rotates 120°. **C:** biloculine mode of coiling: the

coiling axis does not rotate.
a: aperture; **cax:** coiling axis; **chs:** chamber suture; **mt:** miliolid tooth.

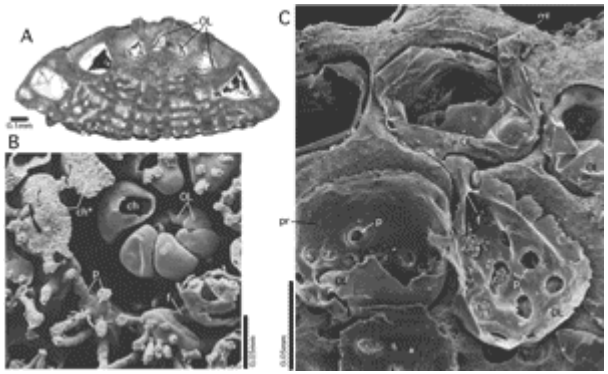


Figure 69: Organic lining.
A: *Lockhartia haimei* (**DAVIES**), megalospheric specimen, axial section, transmitted light micrograph. From the Salt Range, Pakistan. Paleocene. Note the detachment of the organic lining from the inner surface of the biomineralized chamber wall by the first generation of cement deposited during early diagenesis. **B-C:** *Planorbulinella larvata* (**PARKER** et **JONES**). Gulf of Aqaba, Red Sea; Recent. **B:** SEM graph of epoxy resin cast of a microspheric specimen. The subequatorial section of the shell reveals the detail of the early stages of growth, where the resin could not penetrate into the nepionic spiral chambers. After the dissolution of the mineralized shell, the organic lining alone documents the earliest chambers. **C:** megalospheric specimen, equatorial section, etched in order to reveal the organic lining and the lamellation of the chamber walls. The drying of the preparation before its coating for the SEM contracted the organic lining, detached it from the inner surface of the mineralized wall and broke the connection with the organic poreplugs at their weakest spot. This produced the circular holes in the organic lining of the preparation. Note the organic lining that coats the foramina connecting the first three chambers.
ch: chamber; **ch*:** late spiral chamber filled with epoxy resin; **f:** foramen; **ml:** median layer of the primary chamber wall separating the inner from all outer lamellae; **OL:** organic lining; **p:** pore.

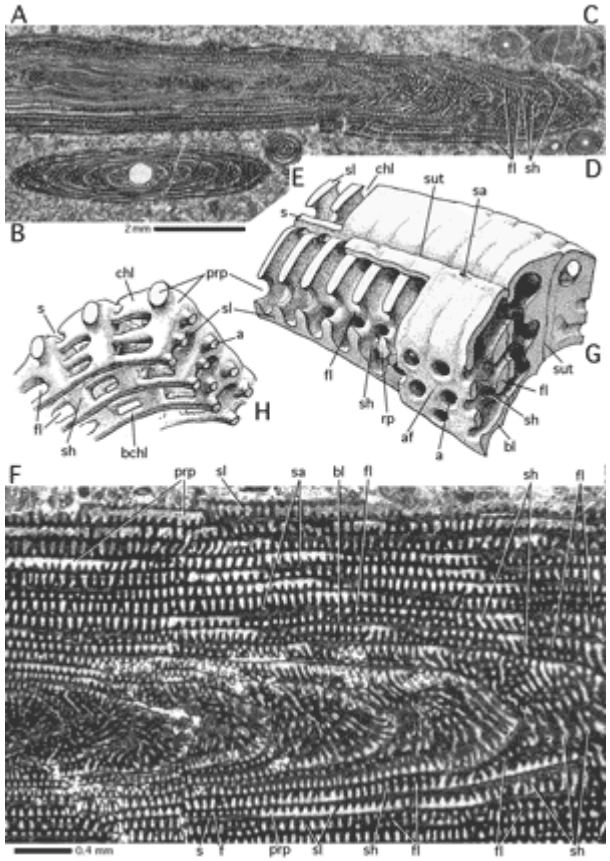


Figure 70: Odd association and polar structures in *Praealveolina tenuis* **REICHEL**. From Alcantara, Lisbon; Cenomanian. Transmitted light micrographs.
A: microspheric specimen, axial section; **B:** megalospheric specimen, axial section; **C-E:** odd partners: **C:** axial section of microspheric *Simplalveolina* sp.; **D:** axial sections of megalospheric *Simplalveolina* sp.; **E:** *Ovalveolina* sp, axial section. **F:** microspheric *P. tenuis*, axial section, detail showing polar structure with floors and shaftsin the basement. **G:** model of two subsequent chambers near their polar ends where the first floors in the basement appear. **H:** model of the protoplasmic body filling the cavities in G. Both models schematic, not to scale, after **REICHEL**, 1933.
a: aperture: **af:** apertural face; **bchl:** basement chamberlets; **bl:** basal layer; **chl:** (main) chamberlets; **fl:** floor; **prp:** preseptal passage; **rp:** (incipient) residual pillar; **s:** septum; **sa:** supplementary aperture; **sh:** shaft; **sl:** septulum; **sut:** cameral suture.

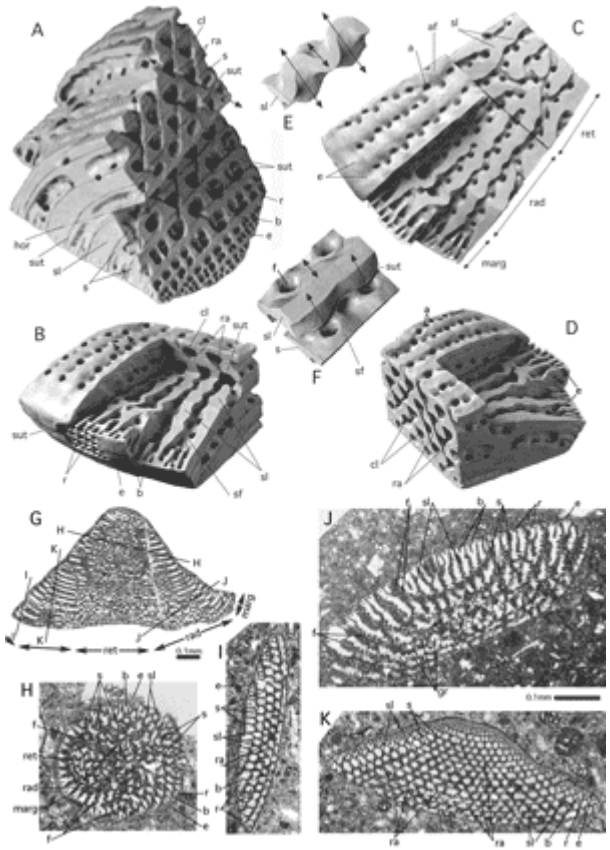


Figure 71: The structure of *Orbitolina*.
A-D: Oblique and vertical views of the cone base. These plasticine models sculptured in the years around 1955 by **M. REICHEL** (* 1896 - † 1984) were never published. **E-F:** Details of a septulum in the radial zone of the discoidal chamber. In model E the septulum is cut below the roof and above the bottom of the chambers. The apparent folding of the section results from the adjustment of the endoskeletal structure to the crosswise-oblique arrangement of the stolon axes (arrows) that produce so-called ramps. In model F the septulum is cut in the middle of the chamber and shows a part of the chamber bottom with the face of the previous chamber. In the middle of the chamber, the section of the septulum appears unfolded. Compare Fig. 47H and Fig. 80G. **G-H:** Random thinsections of *Orbitolina* sp. from Southwestern France, Albian. Transmitted light micrographs. In Fig. G the approximate positions of sections H-K are indicated. Note the inverse orientation: the sections face downward. **G-K:** Random sections of *Orbitolina* sp. from Southwestern France, Albian. Transmitted light micrographs. The approximate position of sections H-K are indicated in section G that is very close to the axial plane. For **HENSON**'s zonation of the chamber see Fig. 20. Section H demonstrates details of the reticular zone, section I details of the marginal zone and section J details of the radial zone. The transverse section K shows the ramps produced by the crosswise-oblique stolon system.
a: aperture; **af:** apertural

face; **b:** beam; **cl:** chamberlet; **e:** epiderm; **f:** foramen; **gr:** coarse grains in the septum that obscure the structural pattern; **hor:** horizontal section in the plasticine model; **marg:** marginal zone; **r:** rafter; **ra:** ramp; **rad:** radial zone; **ret:** reticular zone; **s:** septum; **sf:** septal face; **sl:** septulum; **sut:** suture of the chambers. Double arrows in E and F: crosswise oblique foraminal axes.

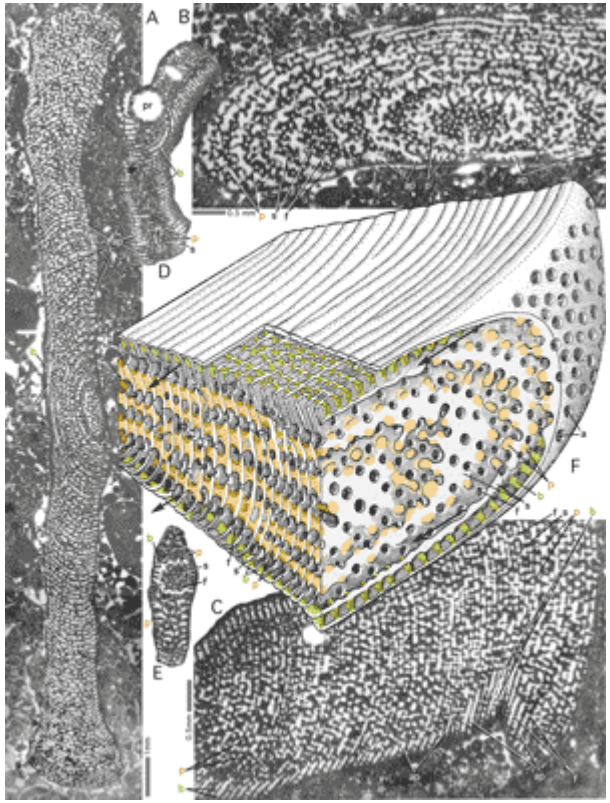


Figure 72: The structure of *Orbitopsella*: a simple exoskeleton and a pillared endoskeleton in a discoidal shell: *Orbitopsella dubari* **HOTTINGER**, Bou Dahar, Eastern Morocco, Middle Lias. Transmitted light micrographs.
A: oblique section of complete microspheric specimen; **B:** oblique section of microspheric specimen. The septa of the thickened margin are cut tangentially and reveal the alternating pattern in the disposition of foramina on the septal face. **C:** oblique tangential section of a microspheric specimen at a low angle to the equatorial plane showing a part of the disc with its exoskeleton (restricted to beams). Note the large open spaces, the lateral annular passages (**arrows**), that separate exoskeleton and endoskeleton. **D:** Oblique centered section of megalospheric specimen. Note the structured wall of the embryo, that shows it to be a sphaeroconch. **E:** Transverse section (parallel to the axis of coiling) of a megalospheric specimen. The septum in this tangential section reveals the alternating pattern of the apertures. **F:** schematic model of structure after **HOTTINGER**, 1967; not to scale.
Green: exoskeleton; **brown:** endoskeleton.

a: aperture; **ap:** annular passage; **b:** beam; **f:** foramen; **p:** pillar; **pr:** sphaeroconch; **s:** septum.

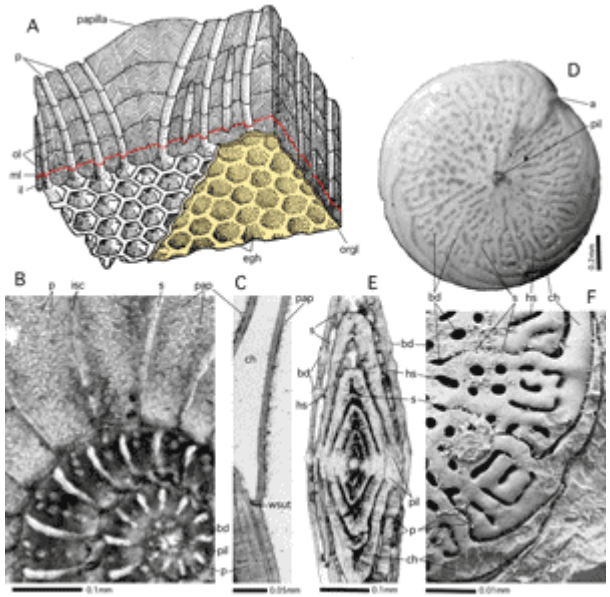


Figure 73: Papillae, beads and axial piles of lamellae.
A: papilla and pores. Stereograph, schematic, not to scale; after **HOTTINGER**, 1977. **B-C:** *Assilina madagascariensis* (d'**ORBIGNY**) from Mauritius. Recent. Transverse section parallel to equatorial plane (B) and axial section (C) with minute papillae on the last whorl; transmitted light micrograph. **D-F:** Beading in *Amphistegina papillosa* **SAID**. Gulf of Aqaba, Red Sea; Recent. **D:** dorsal view of shell showing beading of septular and hemiseptular sutures. Incident light micrograph. **E:** axial section showing hemiseptular and septular support of beads; transmitted light micrograph. **F:** Epoxy resin cast of shell cavity showing spiral main chamber lumina in dorsal view, interrupted by the hemiseptula supporting the interseptal beads, SEM graph.
a: aperture; **bd:** beads (septular and hemiseptular); **ch:** main (spiral) chamber lumen; **egh:** eggholders; **hs:** hemiseptulum; **il:** inner lamella; **isc:** intraseptal canal system; **ml:** median layer; **ol:** outer lamellae; **orgl:** organic lining of protoplast; **p:** pores; **pap:** papillae; **pil:** axial pile of lamellae; **s:** septum and septal suture; **wsut:** whorl suture.

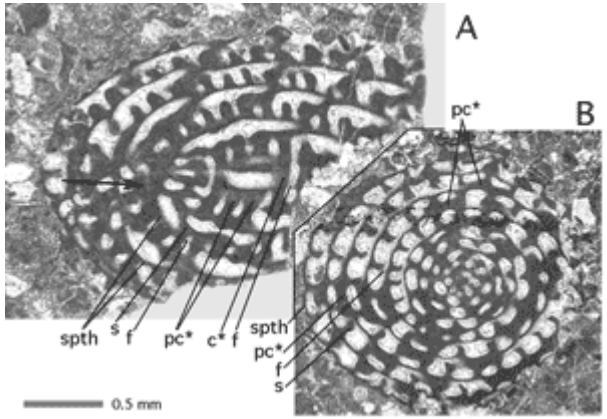
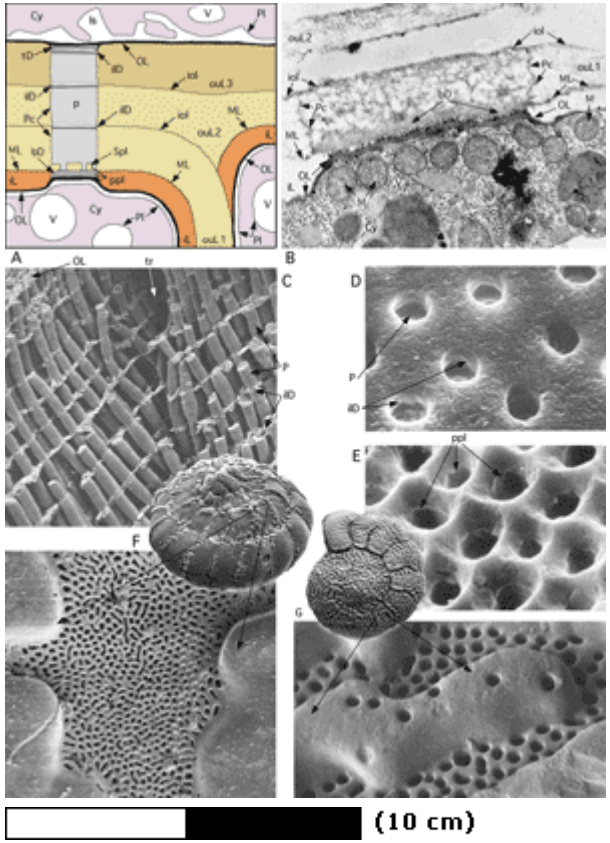


Figure 74: Parachomata in *Pseudodoliolina* sp. from a commercial thin section labeled "Moscow", Permian.
A: oblique section at low angle to axis of coiling (arrow). **B:** oblique section nearly perpendicular to the axis of coiling.
c*: choma; **f:** foramina forming a single row in alternation with the parachomata; **s:** septum (without fluting); **spth:** spirotheca (no trace of keriotheca).



The magnification of each figure is in proportion to the length of the 10 cm scale bar above.

Figure 75: The pore and its organic constituents. **A:** a pore in an inner chamber covered by an outer whorl, according to **LEUTENEGGER** (1977), schematic, not to scale. **B:** Accumulation of mitochondria below a pore mouth in *Bolivina* sp., thus indicating the pores' main function: gas exchange. TEM micrograph of a section oblique to the surface ot the wall that exaggerates the thickness of the pore discs. The detachment of the outer lamella 2 (ouL 2) is an artifact of preparation. x 24,000. Courtesy **S. REBER-LEUTENEGGER**. **C:** Resin cast of pores in the lateral chamber wall of *Nummulites partschi* **DE LA HARPE** with trabeculae. The carbonates of the shell are dissolved with HCl. SEM graph x 1,000. **D:** Outer pore mouths in the lateral suface of chamber wall of *Assilina*. Note the annular attachment of the interlamellar discs. SEM graph x 5,000. **E:** Inner pore mouths in the lateral chamber wall of *Assilina* shaped as eggholders (in order to keep the symbionts below their breathing chimneys). Note the annular suture of the pore plug. SEM graph x 5,000. C-E from **HOTTINGER**, 1977. **F:** Perforation pattern on the dorsal surface of *Challengerella persica* (Recent, Persian Gulf): densely perforated porefields between imperforate ornamentation. SEM: oblique dorsal view of shell, x 30, and detail of porefield, x 500. **G:** Perforation pattern in *Ammonia reyi* **MARIE** (Pliocene, Dar bel Hamri, Northern Morocco): densely perforated

porefields between loosely perforated ornaments. SEM graphs of dorsal shell view (x 30) with detail (x 500). **F-G:** from **BILLMAN** *et alii*, 1980. Abbreviations: **bD:** basal (pore) disc; **Cy:** cytoplasm; **iL:** inner lamella; **iID:** interlamellar disc; **iol:** interlamellar organic lining; **ls:** lacunar system (in the cytoplasm); **M:** mitochondria; **ML:** median layer separating inner from outer lamellas; **OL:** Organic lining (here difficult to separate from plasmalemma of host); **ouL 1:** primary outer lamella; **ouL 2, 3:** subsequent outer lamellas; **P:** pore; **Pc:** organic pore coat; **Pl:** plasmalemma; **ppl:** pore plug (note its porosity); **Spl:** (biomineralized) sieveplate; **V:** vacuole.

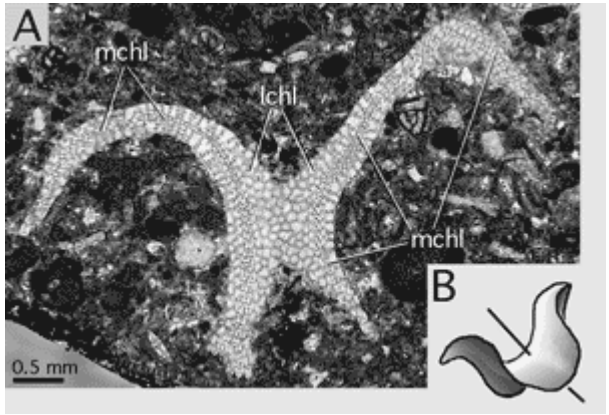


Figure 76: A: selliform deformation of the lenticular-compressed test of *Eulepidina* sp., Oligocene, Sarawak, Borneo. Transverse section approximately perpendicular to the axis of the shell. Transmitted light micrograph. **B:** sketch of a selliform shell with its axis. Schema, not to scale.

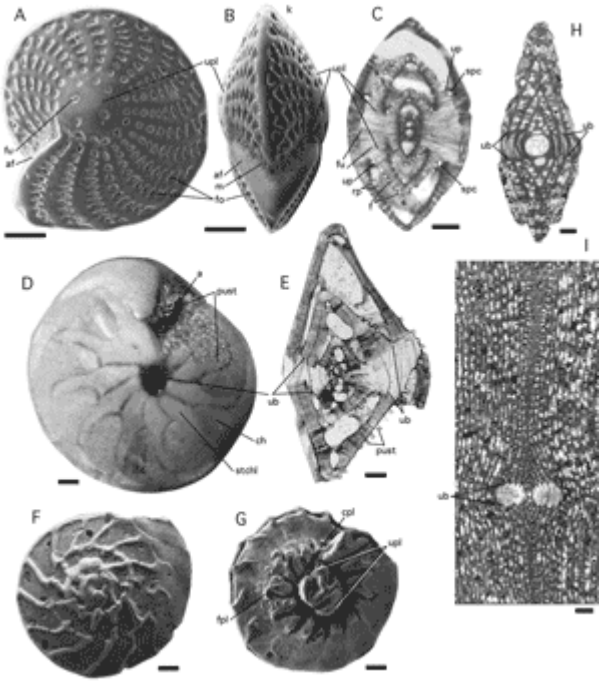


Figure 77: Umbos and umbilical plugs.
A-C: *Elphidium craticulatum* (**FICHTEL** et **MOLL**) from the Gulf of Aqaba, Red Sea. Recent. **A:** lateral view, SEM graph. **B:** peripheral view, SEM graph. **C:** slightly oblique axial section cutting through the symmetrical pair of umbilical plugs. Note the presence of spaces in the biumbilical shell, caused by spiral canals and funnels. Transmitted light micrograph. **D-E:** *Amphistegina lessonii* d'**ORBIGNY** from the Gulf of Aqaba, Red Sea. Recent. **D:** ventral view shows the stellar chamberlets overgrowing part of the ventral umbo. Incident light micrograph. **E:** axial section of specimen having lost the last few chambers. There is a smaller dorsal and a larger ventral umbo. **F-G:** *Ammonia umbonata* (**LEROY**). Dorsal and ventral views, SEM graphs. The ventral (umbilical) view exhibits a free-standing, composite umbilical plug. **H-I:** the umbos in porcelaneous shells may react to diagenetic processes by differences in recrystallisation that possibly indicate a differentiation in the texture of the wall in the umbonal area of the shell. Diagnostic for the involute stages in the growth of Meandropsinidae in the Upper Cretaceous of the Pyrenean Gulf. **H:** megalospheric *Fascispira* sp. from Canelles, Lerida, Northern Spain. Axial section. **I:** microspheric *Larrazetia larrazeti* (**SCHLUMBERGER**), center of axial section, from Bac de Grillera, Northern Spain. All scale bars 0.1 mm.
a: aperture; **af:** apertural face; **cpl:** coverplate; **f:** foramen; **fo:** fossette; **fpl:** foramenal plate; **fu:** funnel; **k:** keel; **m:** mask; **pust:** pustules on amphisteginid face; **rp:** retral process; **s:** septum; **spc:** spiral canal; **ub:** umbo; **up:** umbilical plate; **upl:** umbilical plug.

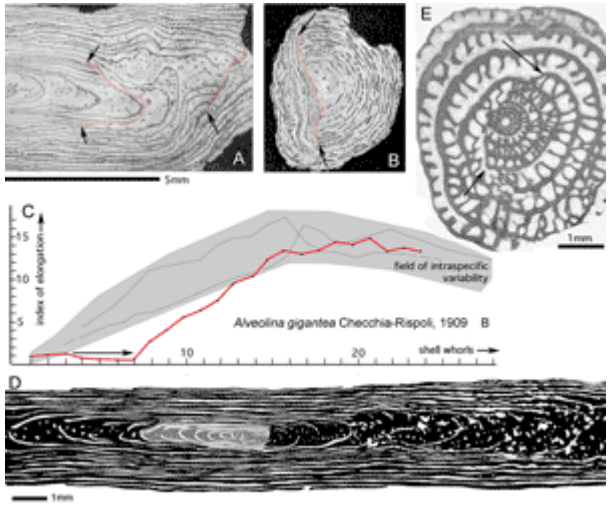


Figure 78: Regeneration in fusiform-elongate shells: **A-D:** *Alveolina gigantea* **CHECCHIA-RISPOLI**. Microspheric generation. Palermo, Sicily, Middle Eocene. **E:** *Pseudoschwagerina* sp., megalospheric specimen, from Palazzo Adriano, Sicily, Permian.
A: a fragment of the polar realm of the shell cut in the axial direction shows two periods of regeneration (red lines designated by arrows) during late ontogeny. **B:** a similar fragment cut in a direction perpendicular to the shell axis, with one broken surface, that has been regenerated in an attempt to restore the cylindrical shape of the shell. At such a late ontogenetic stage the original shape of the shell can not be regained through regenerative growth. Incident light micrographs. **C-D:** regeneration at an early stage of ontogeny: **C.** the rate of elongation was higher in the regenerated half of the shell (red curve) than in the undisturbed half, until the range of elongation that is characteristic for the species was attained again. Note the absence of elongation index increase in the early whorls broken away (arrow). Data from **HOTTINGER**, 1962. **D.** Compare the camera lucida drawing of an axial section: broken early shell in gray, regenerated shell in black. **E:** in a fusulinid the regeneration of the broken whorls 3-6 produces an almost perfect equatorial spiral after only two more whorls of growth.

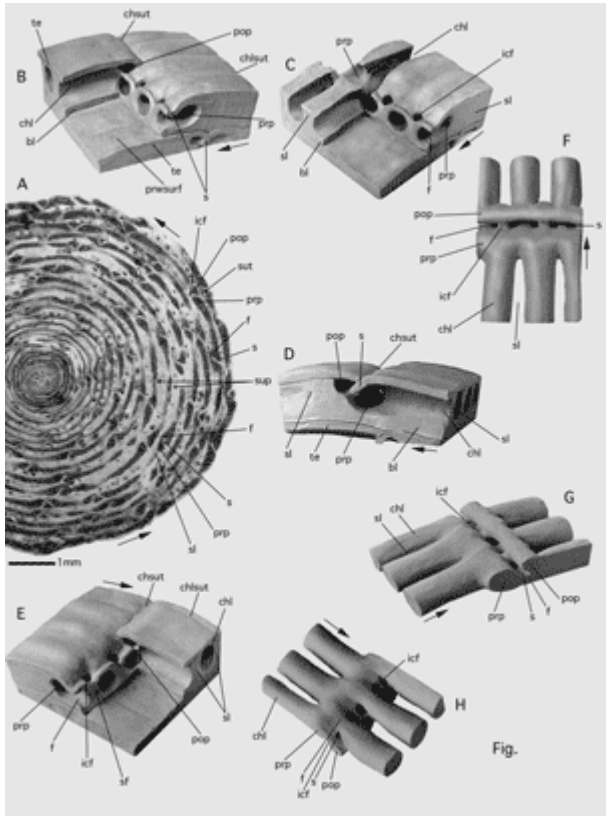


Figure 79: Preseptal (**prp**) and postseptal (**pop**) passages.
A: *Alveolina munieri* **HOTTINGER** (equatorial section of microspheric specimen, Middle Lutetian, S. Giovanni Ilarione, Northern Italy). **B-E:** unpublished plasticine models of the shell by **M. REICHEL**. **B-C:** oblique views showing chamberlets. In **C** the chamber roof (spirotheca) is partly removed. **D:** side view of chamber showing septum and passages behind and in front of it. **E:** oblique view complementary to B showing main and intercalary apertures. the septal realm between two adjacent chambers. **F-H:** unpublished models of sarcode (=shell cavities) by **M. REICHEL** seen from above (F), obliquely from the side (G) and from below (H); **Arrows:** direction of growth.
bl: basal layer; **chl:** chamberlet; **chlsut:** chamberlet suture; **chsut:** chamber suture; **f:** foramen; **icf:** intercalary foramen; **pop:** postseptal passage; **prp:** preseptal passage; **prwsurf:** chamber roof surface of previous whorl; **s:** septum; **sl:** septulum; **sup:** supplementary passages in basal layer; **sut:** suture (of chambers); **te:** chamber roof (tectum).

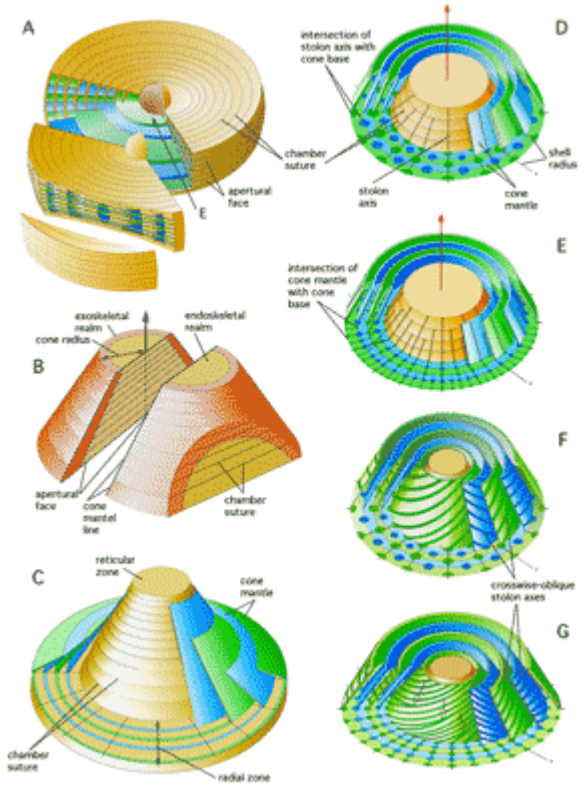


Figure 80: Stolon planes and foramenal axes in discoidal-annular and conical-uniserial shells. Schematic, not to scale.
A: Discoidal shell with a broadening periphery. Green and blue stolon planes are added step by step to the equatorial plane (E) as the shell margin thickens during ontogeny. The sector cut from the disc is cut in its turn in a transverse direction. **B:** A cone composed of a single series of discoidal chambers of which the marginal and axial areas are differentiated by colour. Note the distribution of the marginal area, the emplacement of the exoskeleton, and of the axial area housing the endoskeleton, in axial, horizontal (basal) and transverse sections. The axis of the shell is indicated by a vertical arrow. The surface of the cone is called the **cone mantle**, its horizontal termination is the **cone base**. A vertical line on the slanting surface of the cone is called a **cone mantle line**. The **cone radius** is indicated by a double arrow. **C:** The stolon axes are distributed on cone mantles in conical- uniserial foraminifera. If the cones increase their radial dimension markedly during growth, additional cone mantles are added in order to maintain the radial distances between the cone mantles relatively constant. This addition of cone mantles disturbes the regularity of the endoskeletal structures. In the models D-G, the addition of cone mantles during ontogeny is not taken into account. **D-G:** arrangement of stolon axes on cone mantles in the so-called radial zone of the cone (Fig. 20) is in accordance with the four basic patterns that govern discoidal structures. In conical shells, however, the stolon planes are replaced by cone mantles. As the cone increases in radius during growth, new stolon axes are intercalated in the cone mantles (arrows). **D:** stolon axes in the cone mantles alternate in

radial position as a mantle is added, *e.g. Dictyoconus*. **E:** arrangement of stolon axes on cone mantle lines aligned on a cone radius. **F:** crosswise-oblique arrangement of stolon axes alternating in radial position on successive cone mantles. **G:** crosswise-oblique arrangement of stolon axes in line on a shell radius on subsequent cone mantles. This structure is a characteristic of *Orbitolina* (Fig. 71).

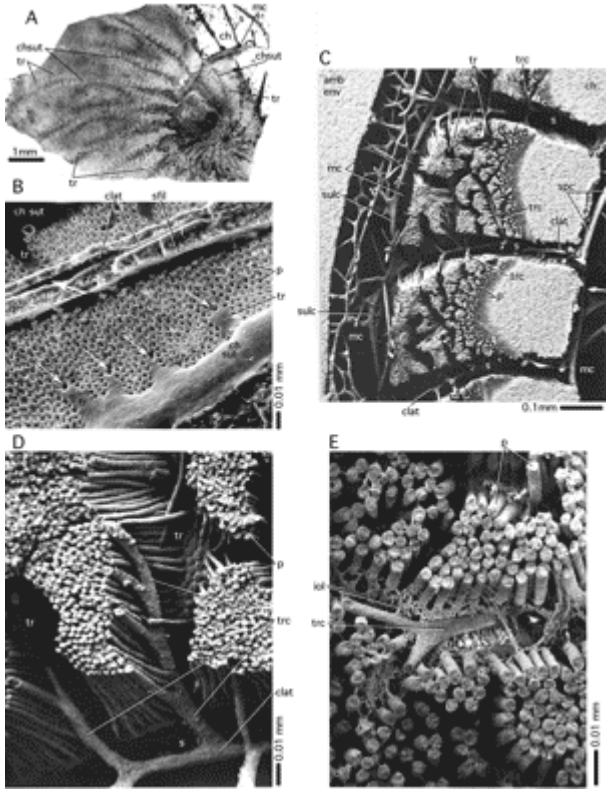


Figure 81: Trabeculae.
A: trabecules in a totally evolute nummulite, *Nummulites giganteus* (**MAYER-EYMAR**). Crimea. Lower Eocene (Cuisian). Transmitted light micrograph of a section tangential to the lateral chamber walls. **B-D:** unfilled shells of *Nummulites planulatus* (**LAMARCK**) from Bos d'Arros, Gan, Southwestern France, Cuisian. **B:** lateral surface of the shell with a part of a septal suture between alar prolongations and their extensions, the trabeculae. The white arrows indicate the orifices of the trabecular canals. The lateral surface is overgrown by the next whorl that has been broken away above the basal suture of a septum of an alar prolongation leaving a linear mark called septal filament. At the base of the septum of an alar prolongation there is a single intraseptal canal running the lenght of the alar prolongation. Where such a canal crosses a trabecular orifice (arrow), a passage may be created by partial resorption of the wall. This passage connects canal cavities of two successive whorls. SEM graph. **C:** epoxy-resin cast of shell cavities cut in an approximately equatorial direction showing two complete chambers with their

marginal cord. Note the "grooves" in the porous wall created by the trabecular canals. SEM graph. **D:** detail of C showing the deviation of the pores in order to admit a trabecular canal. **E:** trabecular canal in *Nummulites partschi* **DE LA HARPE** from Bos d'Arros, Gan. Cuisian. Epoxy resin cast. The preservation of the interlamellar organic lining as a cavity in the shell permits the oblique path of the trabecular canal to be followed through subsequent lamellae.
Abreviations: **amb env:** ambient environment appearing in a cast of cavities as solid mass; **ch:** chamber lumen; **chsut:** chamber suture; **clat:** lateral intraseptal canals in the chamber and in the alar prolongations; **iol:** interlamellar organic layer; **mc:** marginal cord; **p:** pores; **sfil:** septal filament; **spc:** spiral canal; **sulc:** sulcus; **tr:** trabecule; **trc:** trabecular canal.

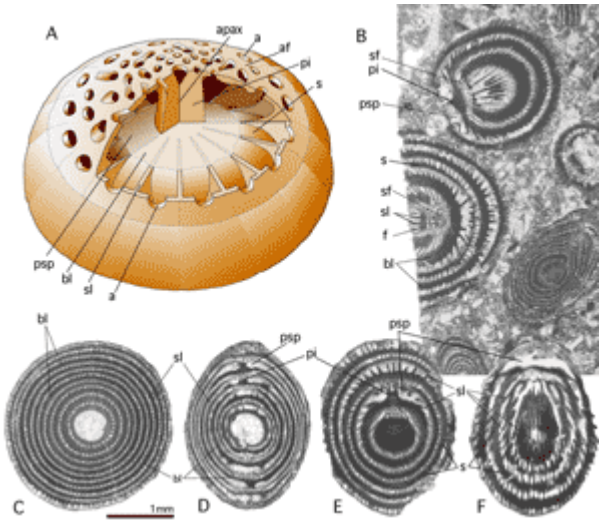


Figure 82: Trematophores.
A: stereograph of the trematophore of *Lacazinella* supported by a single residual pillar in axial position. Schema, not to scale. **B-F:** *Lacazinella wichmanni* (**SCHLUMBERGER**) from the Vogelkop, New Guinea. Middle-Upper Eocene. Transmitted light micrographs. All specimens are megalospheric. **B:** sections tangential to a septal face. **C:** a section perpendicular to the apertural axis reveals the concentric growth of the chambers from their beginning. **D:** section in the apertural axis. Note the alternation of the trematophore on opposite poles of the shell in successive chambers. **E:** oblique section cutting the apertural axis in a pillar supporting the trematophore. **F:** oblique section not cutting the apertural axis within the shell. Note the interruption of the septula below the equatorial roof of the chambers.
a: aperture; **af:** apertural face; **apax:** apertural axis; **bl:** basal layer; **f:** foramen; **pi:** pillar; **psp:** preseptal space; **s:** septum by transformation of the outer chamber wall that is totally covered by a new concentric chamber; **sf:** septal face; **sl:** septulum.

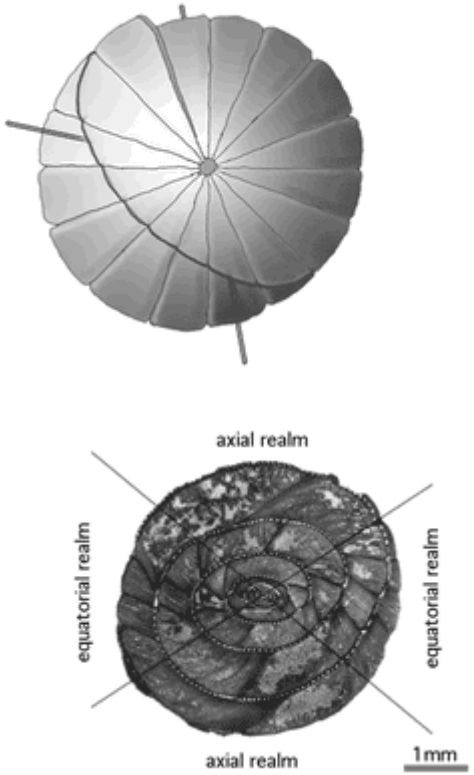


Figure 83: Model in polar view and a globular *Alveolina* (Middle (?) Eocene of Pakistan) cut in a similar direction. Note the shortened distance between the septa in the equatorial and the lengthened distance in the axial realm. In oblique sections of globular to elongate involute planispiral shells the structure of the chambers in opposite sectors of the section approaches more or less closely in appearance that of either an equatorial or an axial section depending on the location and angle of the cut with respect to the septa.